A TEXTBOOK OF ENTOMOLOGY

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by

HERBERT H. ROSS

Systematic Entomologist,
Illinois State Natural History Survey;
Professor of Entomology, University of Illinois.

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With deep appreciation for his guidance, encouragement, and patience, this volume is gratefully inscribed to Professor George J. Spencer, who opened the door of entomology to me.

Preface

It seems to me that there has been an increasing need for an introductory textbook that would bring under one cover the fundamental aspects of entomology, organized so as to give students a general idea of the entire field. This book has been written with this aim in mind.

Much detailed information has been purposely omitted in the hope that the basic principles would not be obscured. It is thought that this would serve better the needs of both entomological students desirous of specializing later in certain fields and students in other branches of biology desiring a general understanding of entomology for background information.

Too often entomology has been presented with no explanation as to its development. The chapter on the growth of entomology has been designed to outline the development of the science in terms of basic causes rather than to present a long list of dates and names. Another field often neglected is the rich one of paleontology. In the presentation of the chapter on geological history no attempt has been made to achieve completeness taxonomically, but rather to give a picture of the dynamic rise of insects in relation to the forces surrounding them.

In the interest of simplicity, physiology has been segregated as a separate chapter, following a treatment of external and internal anatomy. In this way it has been possible to organize physiology by function, rather than structure, since the former is much easier for students to follow. A word of caution is in place regarding the keys to orders and families. These are designed to accommodate only common members of common families and hence are far from complete. They are intended primarily to aid beginning students in realizing the type of differences used in delimiting orders and families and to give them practice in the actual manipulation of keys.

I am greatly indebted to many persons who have discussed choice of material and organization of the contents or have read portions of the manuscript and made criticisms of value. Of especial help in this capacity have been the late T. H. Frison, and W. V. Balduf, B. D. Burks, G. C. Decker, D. M. DeLong, W. P. Hayes, Harlow B. Mills, C. O. Mohr, M. W. Sanderson, Kathryn M. Sommerman, Roger C.

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HERBERT H. ROSS

Illinois Natural History Survey,
Urbana, Illinois

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Growth of North American Entomology

Man has always had his troubles with insects. When he first emerged as man he already had fleas and lice and was fed on by mosquitoes and pestered by flies. In those early days, when human populations were scattered and sparse, man's struggle was on a primitive plane—to find natural food from day to day and to escape the onslaughts of predatory animals. At this period it is doubtful if insects and insect-borne diseases were nearly as important deterrents to man as were other inimical factors of the environment. In fact, on the average, insects were probably of great help, because termites, grasshoppers, grubs, and the like could be found and eaten when other foods were not obtainable.

From primeval conditions man's progress has been based essentially on changing various factors of his environment and making it better suited for his own survival and increase. But every change that benefited man also benefited a host of insects. Gradually, as the more stark enemies of primeval life, such as the leopard and tiger, ceased to be a great threat to primitive man, insects became increasingly important as a challenge to his success.

In the first place, increase in human populations allowed a great increase of such insect ectoparasites as lice and fleas. This was due to the ready accessibility of additional host individuals for the insects and, therefore, better opportunities for dissemination and chances for reproduction. The same factors favored the increase and spread of pestilence, including insect-borne diseases. When large cities arose, they were repeatedly swept by outbreaks of these maladies, in the same way that Imperial Rome was decimated by bubonic plague in the second century A.D.

Insects became a real factor with food as with health. When man began to store food, it was attacked by a host of insects which before had been of no significance in the human environment. In the tremendous food-storage organization of today, insects destroy thousands of tons of food annually in spite of widespread and expensive control programs.

When populations outstripped the food-producing capacity of natural surroundings, man domesticated animals. The concentration of these allowed an increase of their ectoparasites and diseases, thus partially nullifying the effort to enlarge the food supply. The cultivation of crops brought about the greatest change with regard to insects. Agriculture congregated plant hosts so that their insect attackers could build up extensive populations on them. The Egyptian writer in the time of Rameses II (1400 B.C.) commiserates with the peasant that "Worms have destroyed half of the wheat, and the hippopotami have eaten the rest; there are swarms of rats in the fields, and the grasshoppers alight there." In the more recent period of crop improvement, new varieties of plants developed for increased yield have frequently been more attractive to certain insects than original wild hosts, with a resultant influx of destructive forms to the cultivated crops.

This situation has been made more serious by man's development of transportation between all parts of the world. Insects of many species have been carried to continents new to them, where they have found favorable climates, succulent acceptable cultivated hosts, and a freedom from the natural enemies which had kept their numbers in check in their original homes. Sometimes the result has been disastrous, as, for example, the entry of the European corn borer and the Japanese beetle into North America. These two species are of little economic importance in their native range, but in the United States they have caused losses to crops in the magnitude of millions of dollars per year.

North America has been especially hard-hit by losses due to insects. This is the result of the cultivation here in recent centuries of many crops not indigenous to the area, to introduction of many new pests, and to changes wrought by agriculture that have favored many endemic insect species. Losses of crops, stored products, domestic products, and other commodities were estimated in 1938 at $1,258,000,000 for the United States alone. In addition there is to be considered illness and deaths due to insect-borne diseases, and secondary infections, sickness, and discomfort that result directly from insect bites. This was estimated in 1938 as a cash loss of about $166,000,000. On the basis of these figures, insect damage in this country totals an estimated annual sum of $1,424,000,000.*

A review of insect damage gives the entire group a sinister aspect. But the adage, "There is some good in everything," finds a real place even among this group of apparent despoilers. Many kinds of insects are definitely beneficial. The most conspicuous example is the honey bee, which not only produces a marketable crop of high cash value, but also pollinates many valuable plant species. Many crops, including most of our fruits and legumes, are dependent for pollination on a large number of insect groups such as bees, moths, flies, and beetles. Without these insects we would have no apples, pears, peas, beans, and seeds of other insect-pollinated plants.

Another group of economic insects on the beneficial side of the ledger embraces a large assemblage of parasitic insects whose hosts are other insects. These include ichneumon flies, parasitic wasps, parasitic flies, and many predaceous kinds such as the ladybird beetles. The adults or larvae of these species prey on or parasitize many important insect pests. In some cases they can be used as an efficient control method. The Vedalia ladybird beetle, for example, is one of the chief means of combating the cottony cushion scale, an insect destructive to citrus orchards in California.

Man's efforts to combat destructive insects and control beneficial ones form a field of activity called applied entomology. It is comparable in many ways to the field of medicine that has arisen out of the challenge to combat sickness and disease. In North America, applied entomology involves a financial outlay of considerable proportions. Over two thousand persons are employed primarily in the investigation of economic species and the development of control measures. Many firms make a specialty of manufacturing insecticides or apparatus for their application. In the United States alone $25,000,000 worth of insecticides were used in 1934, and the total cost of annual control operations was estimated in 1938 as $142,-927,000. It must be remembered that the losses of $1,424,000,000 from insects were in addition to this control program, so that the

* These figures are taken from the last general survey of insect damage, published in 1938 by the Division of Insect Pest Survey, Bureau of Entomology and Plant Quarantine, U.S.D.A., Washington, D. C.

total insect bill in the United States is in the neighborhood of $1,600,-000,000 per year.

Entomology, the study of insects, has developed into a very large division of the animal sciences, owing to the proportions and importance of the applied field. For, whereas the primary objective of applied entomology is the reduction of insect damage, it has long been evident that a wide knowledge of fundamental information is necessary as a foundation for effective control. For this reason there has been an appreciation of basic entomological research in many directions. Some phases seemed of little importance when first started and yet later proved of inestimable value in control problems.

BEGINNINGS OF MODERN BIOLOGY

Because of their tremendous abundance, it might seem that insects would have been used a great deal in the early investigations in fundamental biology. The small size of the average insect, however, mitigated against this. Extremely delicate methods of dissection must be used to study anatomy and physiology, and powerful microscopic equipment is necessary for taxonomic studies of almost any insect group. To a large extent, therefore, the fundamentals of biology were based on observations of larger animals. The early development of entomology was a process of transposing to insect studies principles discovered in related fields. To gain a better appreciation of the growth of entomology in the New World, it is instructive to review the origin and evolution of its parent, modern biology, which arose in the European theater of the Old World.

At the time of the discovery of America by the Spaniards, the progress of world science was barricaded by the "age of authority." In the literature of the times were heated arguments over such matters as the number of teeth in a horse; learned authors were quoted, but apparently no one thought to examine a horse and actually count its teeth.

The subsequent sixteenth and seventeenth centuries, which saw the exploration and early colonization of the Americas, witnessed also the overthrow of authority and the return of observation and experiment in science. Both the explorations and scientific advance had their roots in the same fundamental causes, that in these centuries following the Renaissance men developed again the desire to look and think for themselves.

In the field of the biological sciences, Vesalius' work on human anatomy (1543) rejuvenated observation, and Harvey's proof of arterial and venous circulation of blood (1628) introduced experiment. Together, as Locy says, "they stand at the beginning of biological science after the Renaissance." Introduction of the microscope in the seventeenth century led to the microanatomical works of Malpighi and Swammerdam, and to discoveries of microorganisms with which Leeuwenhoek astonished the scientific world.

During this latter period entomology really started to develop. In fact, 1667 and 1668 may be considered almost its birth date, for in 1667 Redi used insects in demonstrations to test the theory of spontaneous creation. He exposed meat in jars, some covered by parchment, others by fine-wire screen, and some not covered. The meat spoiled and attracted flies. These laid eggs in the exposed meat, resulting in a crop of maggots. Of the two covered jars, no eggs were laid on that covered by parchment, but the flies were attracted to the screen-covered one and laid eggs on the screen, since they could not reach the meat itself. Redi observed in this instance that, when the eggs hatched, maggots appeared on the screen instead of on the meat. He concluded, therefore, that maggots in meat resulted from the eggs of insects, and not from spontaneous generation, as was previously supposed.

In 1668 Malpighi published anatomical studies of the silkworm, and Swammerdam published his first insect studies. These men produced the first accurate studies of insect anatomy, preparing skilled illustrations showing details of minute structures and organs, fig. 1. These model works were the inspiration for later work in insect anatomy.

Another important phase of the biological sciences paralleled these advances. As people began to observe nature, interest awakened in natural history, and books on the subject appeared. Early treatises by Wotton (1552) and Gesner (1551–56) were elemental and general, and were characterized by a lack of discrimination between different kinds of related animals. Imaginary animals of folklore were even given consideration as if they actually existed. Later works by Ray at the end of the seventeenth century were on a sounder basis and introduced a clear species concept of living organisms essentially similar to that understood today. Natural-history museums, fig. 2, came into being, stimulated by the many bizarre and unfamiliar objects brought back to Europe by travelers and mariners. Many of these museums were operated as hobbies by wealthy persons and

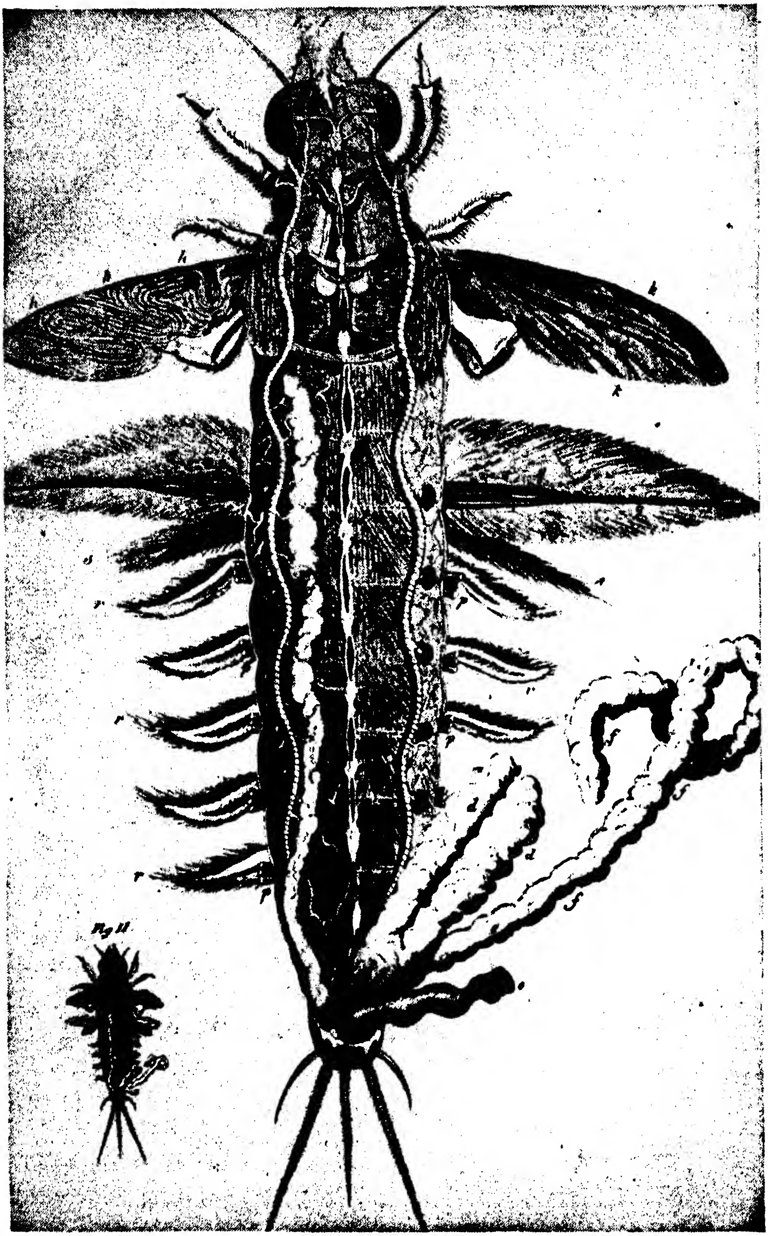

FIG. 1. Anatomy of a mayfly nymph, dissected and drawn by Swammerdam. One of the very early studies of insects, published about 1675. (From Essig, "College Entomology," by permission of The Macmillan Co.)

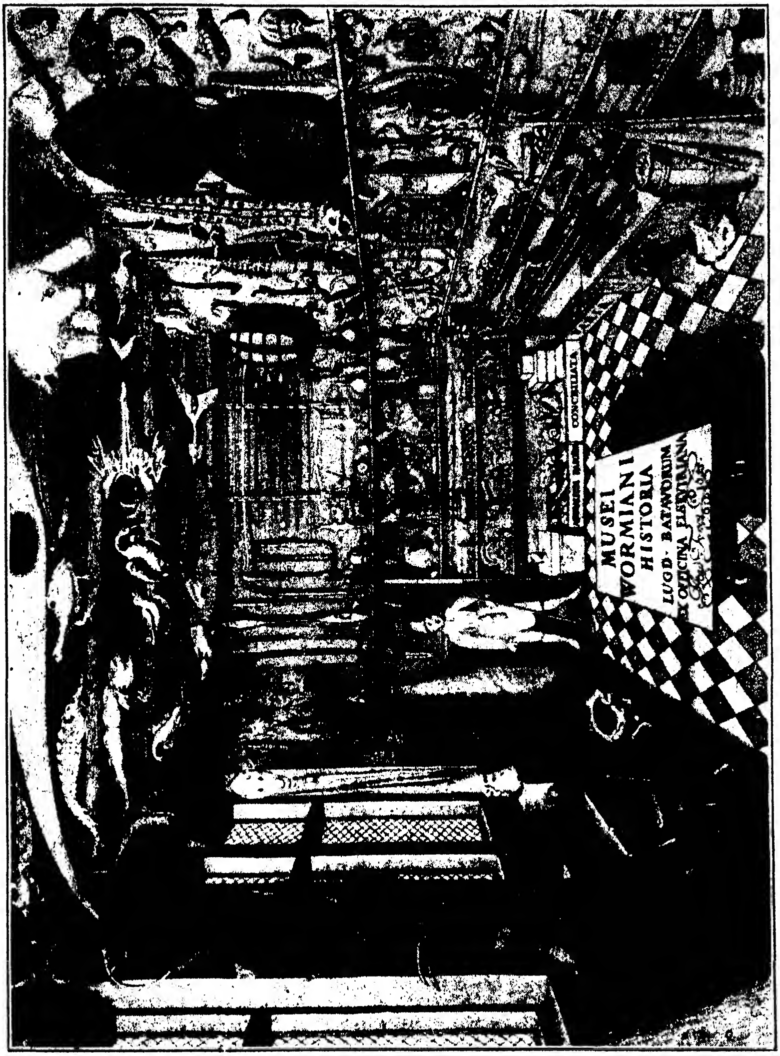

FIG. 2. The famous museum of Olaus Worm, illustrated by its Swedish founder as it appeared in 1655. (Reproduction loaned by Waldo Shumway)

were the forerunners of the extensive private collections which later played an important role in the development of taxonomy.

PROGRESS IN THE EIGHTEENTH CENTURY

Historians picture in the eighteenth century the climax of the revolt against authority, in which despotism and ecclesiasticism were to some extent replaced by the individual asserting his right to be an end in himself. Historical expression of this tide of feeling is found in the American Revolution and the French Revolution. In the United States further expression is found in the rise of universality and state control of education.

In this same century, undoubtedly manifesting the same individualistic trend, the biological sciences in Europe progressed to a new peak. Entomology especially attracted a large number of talented workers. Lyonet, a Hollander, contributed anatomical work of the finest detail, his first and best publication describing the anatomy of the larva of the willow moth (1750). More important in this period from the standpoint of arousing widespread public interest were the voluminous works of the German, Roesel; the Frenchman, Réaumur; and the Swede, DeGeer. All three of these authors published detailed well-illustrated observations on many insects, their life histories, habits, and characteristics.

About the middle of the eighteenth century occurred a movement of extreme importance to the entire field of natural science. It has already been mentioned that John Ray introduced the first clear concept of species. But the names for these species were phrases or descriptions (in Latin), often several lines long, cumbersome, and inconsistently used. In most cases the first name was a noun and corresponded to our present-day usage of a generic name; the remainder of the phrase was adjectival and modified this "generic" name, fig. 3. Various authors in this period began the practice of shortening the adjectival phrase to a single particularly descriptive word, the two then constituting the genus and species of present usage. This is known as binomial nomenclature. In this period the naturalist Linnaeus was coming into prominence as a systematist, organizing the known plants and animals into one of the first comprehensive classifications. In 1758 the tenth edition of his work "Systema Naturae" was published. In this, for the first time, the binomial method of names was employed uniformly throughout a large and comprehensive book. The method proved so successful that workers

(136)

Papilio media, alis pronis, præſertim interioribus, maculis oblongis argenteis perbellè depicta.

SUpina facies intenſiùs & lucidiùs rufa eſt, nervis in alis exterioribus nigris, maculis etiam prope extimum latus majuſculis nigris: interiores alæ ad imum marginem circulos obtinent nigros 4 vel 5 in linea marginis parallela.

Papilio pulla maculis rubris, è rubro albicantibus, & circellis luteis depictis.

ALÆ exteriores ſuperiùs ad extimum latus duas habent maculas oblongas rubras. Non longe ab extimo angulo area lata obliquè tranſverſa, alba rubro diluta; juxta quem circellus niger cum puncto luteo in medio. Interiores alas duo velut ocelli linea lutea pupillam nigram cingente, majore ad exterius alæ latus, minore ad interius. Lineæ nigræ & albicantes alam terminant. Maculæ eædem in pronis quæ in ſupinis alis cernuntur. Color autem non pullùs eſt, ſed rufus, aut fulvus intenſior. Alæ interiores lineam albicantes obliquè tranſverſam ab exteriore latere ad interius deſcendentem obtinent.

Papilio parva nigra duplici in alis exterioribus macula alba inſignis.

E Maculis albis una ad exterius alæ latus, altera ad interius ſita eſt. In prono latere plures maculæ albæ in linea ad alás tranſverſa cernuntur.

Phalæna robuſta rubro & obſcurè citrino & albo coloribus pulchrè depicta.

DOrſum ſeu thorax ſupina de utroque colore participat, ſed de rubro magis. Abdomen ſupinum citrinum lineâ rubrâ mediam ſecundùm longitudinem percurrente. Pronum corpus totum rubet. Alæ ſupinæ exteriores ab exortu lineam habent albam ad marginem deorſum deductam: citrinum colorem rubræ lineæ tranſverſæ diſtinguunt. Alæ interiores parvæ, tum exteriores, tum interiores, circa margines præcipuè latè rubent.

FIG. 3. Part of a page from John Ray's "Historia Insectorum," published in 1710. Note Ray's use of the words *Papilio* and *Phalaena* in a manner comparable to present-day generic names; a short phrase follows, the forerunner of the species name. (Courtesy of the University of Illinois Library)

in all fields adopted it almost immediately. In fact, so profound was Linnaeus' influence on later workers that the tenth edition of his "Systema Naturae" has been designated as the official beginning point for zoological nomenclature. Although Latin is no longer the standard language of science, as it was until the end of the seventeenth century, the Latin names have been preserved and are used for scientific names throughout the world.

Fig. 4. Carolus Linnaeus (1707–1778) at the age of forty. (After Shull)

The stabilization of binomial nomenclature was of tremendous scientific advantage in two ways. First, it gave an easily designated and unambiguous "handle" to species, so that workers in different fields and different countries were able to know better the identity of the species with which others were working. This was of prime importance for integrating advances in comparative anatomy, physiology, and other fields of biology. Second, it provided a system of names which could be expanded indefinitely in a simple manner to accommodate additional genera and species. How necessary to future progress was such a simple method is seen at once by this tabulation: For the entire world Linnaeus recognized about 4500 species of animals, including 2000 species of insects; today over a million and a quarter species of animals are recognized, and of these roughly 900,000 are insects.

Thus taxonomists after Linnaeus were presented with an open invitation to describe and name the myriad of species occurring in all parts of the world. Much of the early work was superficial and has been criticized by many, but it furnished the basis for analyses which led to the formation of the theory of evolution and to the organization of such fields as ecology and limnology.

The field of insect taxonomy in particular had been handicapped under the old system. After Linnaeus' work it began to emerge as a specialized subject. The first outstanding insect taxonomist was Fabricius, a Danish student of Linnaeus. Fabricius' first work, "Systema Entomologica," appeared in 1775; others followed from 1782 to 1804. Fabricius treated the entire insect fauna of the world. By the end of his career it became apparent that this was too large a unit for intensive study by one person. As a result, many workers of the early nineteenth century following Fabricius studied either only one of the larger insect groups or the fauna of only one country.

The works of Réaumur, Linnaeus, DeGeer, and Fabricius stimulated a tremendous development of taxonomic study of insects among European entomologists. They also served as the most important basis for the beginning of entomology in North America.

DEVELOPMENT OF NORTH AMERICAN ENTOMOLOGY

American entomology came into existence about the beginning of the nineteenth century. For the first two thirds of the century development was slow, witnessing the appearance of scattered pioneer works such as form the backbone of further progress in any scientific movement. But after the Civil War many factors contributed to a hastening of the tempo in entomology in the United States. The resultant demand for entomological investigation found eager and able enthusiasts available, with the result that by the end of the century American entomology had blossomed into a well-balanced science of wide practical and theoretical scope.

Prenineteenth Century Work

Prior to the nineteenth century only small fragments were known about North American insects. Naturalist Mark Catesby (1679–1749) was possibly the first to illustrate North American insects in his book, "A Natural History of Carolina, Florida and the Bahama Islands, containing figures of the Birds, Beasts, Fishes, Insects and Plants." Fabricius named some species, relying on specimens sent to him by various collectors or specimens which had been acquired by private collections in Europe. John Abbott, an Englishman who settled in Georgia, collected much material for European collectors in the period about 1780 and prepared many drawings of insects. The economic losses occasioned by insects were noticed with grave concern by Thomas Jefferson in 1782. He was particularly aware of the damage caused in stored grain and gave a few remarks on the problems of control, pointing out a need for further study. But until a few years before 1800 no concerted effort was evident by residents of the United States to investigate the native insect fauna.

250 NOTES ON VIRGINIA.

and happineſs among the whole. We find it eaſi-er to make an hundred buſhels of wheat than a thouſand weight of tobacco, and they are worth more when made. The weavil indeed is a formidable obſtacle to the cultivation of this grain with us. But principles are already known which muſt lead to a remedy. Thus a certain degree of heat, to wit, that of common air in ſummer, is neceſſary to hatch the egg. If ſubterranean granaries, or others, therefore, can be contrived below that temperature, the evil will be cured by cold. A degree of heat beyond that which hatchis the egg we know will kill it. But in aiming at this we eaſily run into that which produces putrefaction. To produce putrefaction, however, three agents are requiſite, heat, moiſture, and the external air. If the abſence of any one of theſe be ſecured, the other two may ſafely be admitted. Heat is the one we want. Moiſture then, or external air, muſt be excluded. The former has been done by expoſing the grain in kilns to the action of fire, which produces heat, and extracts moiſture at the ſame time: the latter, by putting the grain into hogſheads covering it with a coat of lime, and heading it up. In this ſituation its bulk produced a heat ſufficient to kill the egg; the moiſture is ſuffered to remain indeed, but the external air is excluded. A nicer operation yet has been attempted; that is, to produce an intermediate temperature of heat between that which kills the egg, and that which produces putrefaction. The threſhing the grain as ſoon as it is cut, and laying it in its chaff in large heaps, has been found very near to hit this temperature, though not perfectly, nor always. The heap generates heat ſufficient to kill moſt of the eggs, whilſt

FIG. 5. A page from the 1787 edition of Thomas Jefferson's "Notes on Virginia," written in 1781. A small edition was printed in 1782, a French edition later, and a reprinting in the original form was made in 1787. (From book loaned by Harlow B. Mills)

Pioneering Period, Roughly 1800–66

Work on American insects by American workers began about the turn of the nineteenth century. One of the first workers was W. D. Peck, who published many articles on the injurious insects of the New England states. These articles appeared from 1795 to 1819 in various agricultural journals. The pioneer work on North American entomology was "A Catalogue of Insects of Pennsylvania," published in 1806 by F. V. Melsheimer. The chief value of this little 60-page book was its stimulating effect. Its author, his collection, and his association with later workers were a real aid in opening up the subject. His insect collection, incidentally, was the first comprehensive one to be built up in North America and was ultimately purchased many years later by the Harvard Museum of Comparative Zoology.

Fig. 6. Thomas Say (1787–1834), the father of American entomology. (After Howard, courtesy of U.S.D.A., B.E.P.Q.)

In 1812 a group of enthusiastic naturalists organized the Academy of Natural Sciences of Philadelphia. This nucleus of scientists was the cradle of serious descriptive work in many fields of American biology, and among them was entomology. Thomas Say was the outstanding entomologist of the group. He published the first useful classic in the field, three well-illustrated volumes (1817–28), "American Entomology, or descriptions of the insects of North America." The excellence of this work, together with his other papers on insects, has earned for Say the well-deserved title "Father of American Entomology." Say died at New Harmony, Ind., in 1834.

In 1823 Dr. T. W. Harris of Massachusetts published the first of a series of papers on the life history and economic importance of many insects. Harris was a student of Peck who taught natural history at Harvard, from which Harris graduated in 1815. Harris collected and observed insects constantly, and the breadth of his published work increased. It culminated in 1841 in his monumental "Report on Insects Injurious to Vegetation"; this was twice reprinted and revised, the last time in 1852. Harris received $175 from the State of Massachusetts for this work; this was the first tax-supported entomological program in North America. It was also the first real text of economic entomology, and Harris is justly regarded as the founder of applied entomology in America.

The influence of Say and Harris took root immediately. In a few years a dozen authors published papers on the life history, habits, predations, and control measures of insects.

It is interesting to look back at the remedies in vogue for insect control during that period. It must be remembered that the arsenicals, pyrethrum, DDT, and many other effective insecticides were undiscovered at that time. A few of the standard remedies, to quote from Harris, included "Hand picking; sweeping into pans; spray with whitewash and glue; sulphur and Scotch snuff; fumigation with tobacco under a movable tent; syringe with whale-oil soap solution; soap and tobacco water," and many recommendations for cultural control. We can see in these the forerunners of many control measures recommended today.

FIG. 7. Thaddeus William Harris (1795–1856), the founder of applied entomology in America. (After Howard, courtesy U.S.D.A., B.E.P.Q.)

Interest in agriculture led to the establishment in 1853 of a new Bureau of Agriculture in the Federal Government. This Bureau appointed Townend Glover as Entomologist and Special Agent. Glover's duties were varied, including the preparation of exhibits of agricultural seeds, plants, and fruits, as well as insects. But in addition he did considerable investigational work, especially on the insects attacking orange trees and cotton. Glover had the belief that a picture of an insect is of much greater value than the prepared insect specimen. His greatest entomological efforts were consequently devoted to making copper etchings illustrating the insects of North America.

The farmers' losses caused by insect damage were attracting more and more attention. In response to this, the State of New York in 1854 appropriated $1000 for investigations on insects, especially those injurious to vegetation. Dr. Asa Fitch was chosen for this work, which he continued from 1854 to 1872. He wrote 14 fine reports, the result of a great amount of original observation performed with great care, which made available information on the life history of many insects. After Harris' work, these reports were the next great stimulus for further development of entomological work in the United States. Although such was not his title, Fitch was usually called State Entomologist; in his activities he was this in a very real sense and was the first one in the United States.

While Fitch was at the height of his career, several other entomologists were coming into prominence, including B. D. Walsh and C. V. Riley in Illinois, and E. T. Cresson and A. R. Grote in Philadelphia. Walsh's principal noneconomic work was done from 1860 to 1864, but his great contribution to economic entomology belongs to the account of the last third of the century. Riley, Cresson, and Grote also made their great contributions in this later period.

FIG. 8. Asa Fitch (1809–1878), the first of the State Entomologists. (After Howard, courtesy U.S.D.A., B.E.P.Q.)

The Civil War, which concluded the first two thirds of the century, seems to have had only slight effect on entomological work, most of which was being done north of the actual battle area. Its effects, however, had far-reaching consequences in the years immediately following.

Science in Europe for This Period. While the foundation works of American entomology were being written by Say, Harris, Fitch, and Walsh, two very important series of events were taking place in Europe. These had only slight contemporaneous effect in America but were a great contributing factor to entomological development in the next period.

In the first place, European taxonomists were making needed strides in redefining taxonomic concepts, especially as regards families and genera, to accommodate the huge tide of insect species being discovered in the world. Every large order received some attention, and creditably workable systems of classification were set up for them. European workers had access to libraries and collections far superior to any in America. They prepared keys and illustrated works many of which were simply transposed by later American taxonomists to fit American species of insects.

The second circumstance is one which concerned all biological science. In this period (1800–66) there developed ideas which revolutionized the outlook in the entire field. Up to this point work had been almost entirely descriptive, with scarcely any concept of fundamental laws. Now these came to light in rapid succession. Owen brought forward the idea of analogy and homology of parts; Cuvier and Lamarck founded comparative anatomy; Milne Edwards propounded the idea of division of physiological labor; Müller demonstrated the interrelationship of anatomy and physiology; Schwann and Schleiden demonstrated the cell theory; Bichat founded histology; Von Baer founded modern embryology; and Schultze defined protoplasm. To climax this galaxy of ideas, Darwin and Wallace set forth the theory of organic evolution.

That these discoveries were made in such rapid succession is not strange. Scientists had been on the verge of seeing them for many years, and as soon as one fundamental was discovered it served as a key to unlock the next half-anticipated secret. Together with genetics and bacteriology (both discovered later) these discoveries outlined practically the entire range of known biological laws. These, of course, were as fundamental to basic progress in the study of insects as in the study of any other group of living things.

First Entomology in American Colleges. In the early part of the pioneering period courses in natural history began to appear in various colleges in North America. Until the middle of the century they were meager, mostly theoretical and classificatory. They were given chiefly by lecture, sometimes with demonstrations but with little or no field or laboratory work. This applied in large measure to chemistry and physics also. Louis Agassiz at Harvard was the first teacher in zoology to break away from this and introduce laboratory methods in teaching. The greatest impulse to the laboratory method of teaching, however, was the great upsurge of inquiry following the publication in 1859 of Darwin's "Origin of Species." At about this same period such new institutions as Cornell and Johns Hopkins Universities emphasized the teaching of science. In the United States this was coincidental with the establishment of the "land-grant colleges" in 1862 by the Morrill Act of Congress. This promoted education in agriculture, mechanical arts, and natural sciences. Entomology was included only as a part of biology courses, but the foundations were being laid for the later development of its teaching.

American Expansion Period, Roughly 1867–1900

In the two or three decades after the Civil War, American entomology expanded at a prodigious rate. Many reasons supplemented each other to this end. Important were the following:

1. As a result of the westward migration of thousands of people following the Civil War, agriculture expanded in the Middle West and the states on the Pacific Coast. Devastating insect outbreaks occurred periodically. The demand for entomological assistance for the farmer resulted in the rapid development of both state and Federal organizations in economic entomology.
2. American insect collections and libraries had gradually improved and, with the help obtainable from European literature, opened the door for more extensive and better descriptive work. The fundamentals of biology recently discovered provided avenues for many lines of investigation with insects.
3. Demand for trained entomologists brought about teaching of entomology in colleges and universities.

Economic Entomology. Before the beginning of this period (1867–1900) New York was the only state actively sponsoring entomology, through Asa Fitch. In 1866 Illinois appointed a State Entomologist (although he did not become active until 1867), and in 1868 Missouri followed suit. In Illinois the appointment was given to B. D. Walsh, who had written many fine articles on taxonomic and economic entomology. Walsh met death by accident in 1869 but wrote three reports as State Entomologist before that tragedy. After him J. A. LeBaron occupied the post for five years, followed by Cyrus Thomas from 1875 to 1882, and then by S. A. Forbes. In Missouri the appointment was given to C. V. Riley, who held the post from 1868 to 1876. Riley's annual reports were outstanding, in both scientific content and illustration, and were a tremendous stimulus to other authors.

From 1874 to 1876 the migratory locust invaded a number of the important grain-growing states. This outbreak was studied by Riley, who saw in it the need for action on a national scale against injurious insects. His efforts to secure national legislation persuaded Congress to establish the United States Entomological Commission. This was the first recognition in a broad way that economic entomology was of national importance and dealt with many problems the thorough investigation of which transcended state lines. This Commission had Riley as chief, and A. S. Packard, Jr., and Cyrus Thomas as the

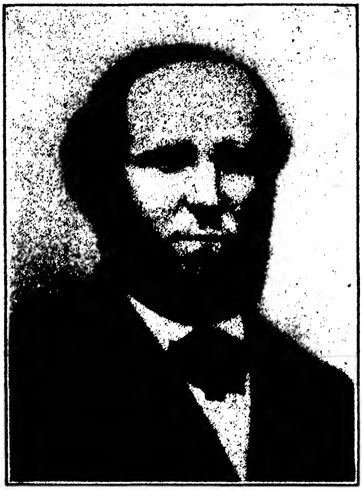

FIG. 9. Benjamin Dann Walsh (1808–1869), an early vigorous writer on various phases of entomology, later first State Entomologist of Illinois. (After Forbes)

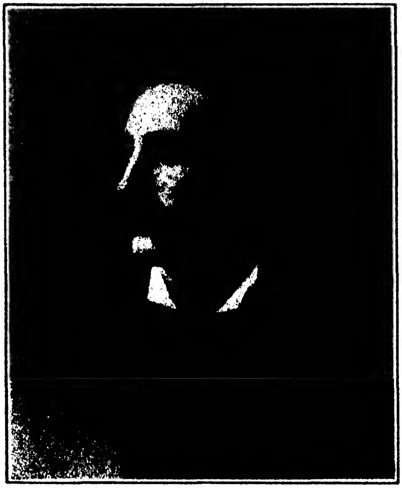

FIG. 10. C. V. Riley (1843–1895), insect illustrator *par excellence,* who first built up the Federal Bureau of Entomology. (After Howard, courtesy U.S.D.A., B.E.P.Q.)

two other members. The Commission was active officially for only three years but did some excellent work and published several extremely useful reports and bulletins. These treated not only the migratory locust but also a wide variety of other economic insects.

For a short period in 1878 Riley succeeded Glover as Entomologist for the Federal Department of Agriculture. J. H. Comstock then held the office for two years, after which Riley again held it, for 15 years. On Riley's return, the entomological work received such support that it was reorganized as a separate Division of Entomology. Under Riley's leadership it rapidly developed into a large and useful organization, with field stations in many parts of the country.

During these years several able entomologists in Canada began writing notable contributions on the insects of that country. The good work of two pioneers stands out conspicuously, that of the Rev. C. J. S. Bethune, who began publishing in 1867, and Dr. William Saunders, whose earliest paper appeared the following year. The efforts of these enthusiasts and others culminated in the founding of the Ontario Entomological Society in 1870 and the establishment of the office of Honorary Entomologist by the Department of Agriculture of Canada in 1884. This post was given to James Fletcher, who in 1887 was transferred to the staff of the Central Agricultural Experiment Station as Entomologist and Botanist. Fletcher had little help and a tremendous territory to cover; that he served the entomological needs of Canadian agriculture so well and so long is proof of his ability and industry. He died in 1908, following an operation.

Until 1887 organized work in economic entomology in the United States was being done only by the Federal Government and by New York, Illinois, and Missouri. Work was also being done by individuals in many other states, from Maine to California. But in 1887 the demands of an ever-expanding agriculture resulted in the Hatch Act, establishing agricultural experiment stations in all states. Investigations of injurious insects were stressed from the beginning, and there arose a need for trained entomologists which far exceeded the meager supply.

The last decade of the century found economic entomology an influential and producing concern. Outstanding work was being done by many workers in the Federal Division of Entomology, notable among whom was L. O. Howard, who in 1894 succeeded Riley as chief. The state organizations (many connected with the agricultural experiment stations) included several brilliant men in their roster. To mention only a few, S. A. Forbes in Illinois, John B. Smith in New Jersey, and E. P. Felt in New York contributed immense amounts of original research and wrote monumental reports, many of lasting value.

Two items of interest had a special effect on entomological thought and procedure in this last third of the century: (1) About 1869 Paris green was discovered to be an effective insecticide, and its success opened up the entire field of stomach poisons for insects. (2) The cottony cushion scale, introduced about 1870 into California, had become such an abundant and serious pest of citrus trees in the '80's as to threaten the extinction of the citrus-growing industry in the West. Known insecticides failed to deter the pest. Finally natural insect enemies of the scale were imported from Australia. One of these, the Vedalia ladybird beetle, destroyed the scale with such persistence that in a few years it ceased to be a problem. Such a wonder-working event established the importance of biological control as a possible means of combating injurious insects.

Insect Taxonomy, Morphology, Etc. During this latter third of the nineteenth century an almost complete foundation was laid for the classification of North American insects. A large number of workers contributed to this, including J. L. LeConte and G. H. Horn on Coleoptera; A. S. Packard, Henry Edwards, and A. R. Grote on Lepidoptera; E. T. Cresson, Edward Norton, and L. O. Howard on Hymenoptera; S. W. Williston, Osten Sacken, and D. W. Coquillet on Diptera; S. H. Scudder on Orthoptera; P. R. Uhler and O. Heidemann on Hemiptera; J. H. Comstock on Coccidae or scale insects; H. C. Osborn on ectoparasites and Homoptera; and many others. In Canada the Abbé L. Provancher was outstanding, especially for his work on Hymenoptera.

These are only a few of the "old masters" who described the first great bulk of the North American insect fauna and gave us our first working synopses. Many outstanding European entomologists also contributed to this literature. It is noteworthy that many of the most outstanding taxonomists of this era and the one that followed were amateur entomologists and made their great contributions as a hobby, without remuneration. To mention a few: LeConte and Horn were practicing physicians, Edwards was an actor, Norton and Cresson were businessmen, Williston a geologist, Provancher a clergyman.

During the decades following Linnaeus different points of view arose regarding many phases of the application of scientific names. As these differences became acute and threatened to nullify by inconsistent usage the benefits of the binomial system, taxonomists of all groups sought measures to bring about uniformity of practice. Success finally crowned their efforts at the International Zoological Congress held at Berlin in 1901, with the adoption by the zoological world of the International Rules of Zoological Nomenclature and the organization of the International Commission of Zoological Nomenclature. It was at this historic meeting that Linnaeus' tenth edition of "Systema Naturae" was designated as the beginning point for zoological scientific names.

Complementary to the development of better literature was the origin and growth of large research collections. Until the end of the first two thirds of the nineteenth century, North American insect collections were relatively small, usually consisting of at most a few thousand specimens. As the complexity of insect identification became obvious, the need became apparent for extensive collections to aid both accurate identification of unknowns and further progress in taxonomy. It was early recognized that accurate identification was essential for sound fundamental research in all fields and for consistent control recommendations. In the United States the first serious effort in this direction was made by Louis Agassiz, who in 1867 appointed Hermann A. Hagen to build up a collection of insects in the Museum of Comparative Zoology at Harvard University. Since then many institutions, including various academies of sciences, universities, and other state and Federal organizations, have stressed extensive insect collections. Many workers maintain personal collections of considerable size. At the present time institution collections in the United States and Canada house a combined total of about 25 million insect specimens, and personal collections probably another two or three million.

FIG. 11. John Henry Comstock (1849–1931), one of the "old masters" in the teaching of entomology in America. (After Howard, courtesy U.S.D.A., B.E.P.Q.)

Teaching of Entomology. Until about 1867 entomology was taught in American colleges only as a portion of courses in biology or natural history. But in 1866 B. F. Mudge gave a course entitled "Insects Injurious to Vegetation" at Kansas State Agricultural College; in 1867 A. J. Cook gave a course in entomology at the Michigan Agricultural College; in 1870 Hagen gave rather informal courses in entomology at Harvard; in 1872 C. H. Fernald began teaching at Maine State College; in 1873 Comstock began teaching at Cornell University; and in 1879 Herbert Osborn taught at Iowa State College of Agriculture. These men were the real founders of the teaching of entomology in the United States. They had little organized or general literature to use as a basis for teaching and, to quote from Osborn, "were feeling their way in the matter of both content and method for entomological instruction."

The task confronting these men was enormous—learning or discovering the multitude of details about insects, including life histories, morphology, development, and classification, and combining it with the then new concepts of general physiology, embryology, phylogeny, and evolution. The splendid and coherent courses which developed from the welding of all this material represent a triumph indeed for these pioneer teachers. Of especial importance in this connection were the early textbooks written by A. S. Packard, who was a trail blazer in this field.

Fig. 12. A. S. Packard (1839–1905), who wrote some of the early entomological works much needed by the American student. (After Howard, courtesy U.S.D.A., B.E.P.Q.)

Creation of the agricultural experiment stations in 1888 led to a tremendous demand for better-trained entomologists for economic positions and stimulated teaching in this field. By the end of the century entomology courses had been organized in most of the leading universities and colleges stressing natural sciences. This was especially true of the land-grant colleges. Outstanding men, such as S. A. Forbes at Illinois, G. A. Dean in Kansas, and M. V. Slingerland at Cornell, set an early example of combining the fundamental and practical aspect in what may be called the first modern courses in economic entomology.

Twentieth Century Developments

In the present century the investigation of all known phases of entomology has progressed and expanded at a remarkable gait. To a large degree this has paralleled appreciation by the public of the tremendous damage caused by insects and the savings to be gained by control of them. This appreciation has been expressed in the form of larger and larger appropriations to support entomological work. Of tremendous aid to entomological studies have been improvement of microscopes, laboratory and field equipment, electric measuring and recording devices of many kinds, gradual improvement of traveling possibilities, and the increase in the number of journals and books for the publication of research results.

Certain phases or definite events have attracted widespread popular attention at various times. Each of these has been a stimulus to further expansion in all fields of entomology. Some of the outstanding items are cited in the following brief remarks.

Medical Entomology. In 1879 Patrick Manson in India discovered that mosquitoes transmit filariasis. In 1889 Theobald Smith in Texas discovered that a tick transmits the organism which causes Texas fever of cattle. In 1898 Ronald Ross in India proved the association of malaria and anopheline mosquitoes. In 1900 Walter Reed and coworkers proved that the mosquito *Aedes aegypti* carries yellow fever. This series of discoveries solved the transmission mystery of some of the world's worst diseases and established the importance of the role insects and other arthropods play in relation to human health. This was the birth of medical entomology. Continued investigation has shown an ever-increasing number of diseases to be primarily insect- or arachnoid-borne, adding bubonic plague, dengue, typhus fever, trench fever, Rocky Mountain spotted fever, African sleeping sickness, and others to the list. For lack of known immunization methods, the medical world has turned in the case of many of these diseases to a control of the arthropod carrier as a means of combating the disease.

Economic Entomology. During the last decade of the nineteenth century and up to the present several insects of foreign origin became established in the United States and Canada and produced catastrophic damage to agriculture. The gypsy moth threatened to wipe out fruit and other trees in the New England States from 1889 to well into the 1900's; the San Jose scale became a country-wide fruit tree scourge before 1900; the destructive cotton boll weevil had invaded the entire cotton belt between about 1895 and 1920; the European corn borer loomed as a possible serious threat to the midwest corn crop in the early 1930's.

Each of these "battles" between the entomologist and a new insect enemy brought forth discoveries of new insecticides, equipment, or methods which frequently had a wide application far beyond treatment of the insect under intensive study. But these discoveries, of course, required more men and more field stations and necessitated coordinated research in insect habits, morphology, physiology, taxonomy, agriculture, bacteriology, and other sciences.

Basic Entomology. The research advances in fundamental fields have followed very closely the demands of the economic entomologist for more and better information about economic insects, suspected species, or related forms. With such a stimulus the number of research workers has increased steadily, and the growth and scope of college teaching have increased with it.

Research in insect taxonomy has followed three principal lines: (1) making keys and synopses to groups not previously treated, (2) restudying groups for which new sets of diagnostic characters have been discovered, and (3) applying to problems of classification more recent biologic or ecologic information and evidence furnished by immature stages. Widespread road systems and the automobile have brought to the entomologist tremendously greater collecting opportunities and have resulted in a rapid increase in knowledge of species distribution.

In this century progress in insect morphology, physiology, embryology, and other fundamental fields has followed a fairly definite pattern. This pattern has been to work out for insects the details of the great biological fundamentals discovered in the nineteenth century. The disconnected anatomical works of Malpighi and Lyonet have been reinvestigated and extended along the lines of comparative anatomy, including histology, morphology, and embryology. Certain insects were found to be ideal subjects for experimentation in genetics and heredity, and in this way much has been learned about both the insects and genetics in general.

Research in insect physiology followed much the same pattern, that is, finding out how the gross functions were carried on in insects in comparison with other animals. In recent years advances in biochemistry and biophysics have opened new fields for investigations in more minute phases of insect physiology. Already discoveries in these new fields have proved of paramount interest, for they are correlating and solving many puzzles of insect physiology in relation to insecticidal action.

In the last two decades many large companies manufacturing chemicals have entered the field of entomology, stressing the development of new compounds toxic to insects or finding better ways to prepare or handle established insecticides. This activity has led into the investigation of fundamental problems of a varied nature, especially in biochemistry and physiology, but also in other fields. So much of this work is being done that this period of entomological history may be characterized by the advent and growth of privately endowed and commercial research and development.

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2

Arthropoda: Insects and Their Allies

Insects belong in the great phylum of jointed-legged animals, the Arthropoda. Of this phylum the insects are a highly specialized group comprising the class Insecta. In the adult stage insects are characterized primarily by having the body divided into three regions, the head, thorax, and abdomen, and by the thorax bearing three pairs of legs. Both the body regions and number of legs are functional groupings of parts, groupings that are very different from those of their original ancestors.

The Arthropoda undoubtedly arose from a wormlike creature very similar in general organization to the Annelida or segmented worms. The body of this ancestor, fig. 13*A*, consisted of a series of uniform segments, each a full ring of the body. The head was a simple structure, probably bearing sensory bristles. The mouth was situated on the ventral side between the head and the first ring or segment of the body. Because of its position in front of the mouth or stomodeal opening, the head region in this early stage is termed the prostomium. Hypothetical steps in the evolutionary progress beginning with this simple stage and leading through generalized arthropods to insects are pictured in figs. 13*A* to 13*F*.

The first great step was the development of a pair of ventral appendages or legs on each body segment, aiding in locomotion, fig. 13*B*. Apparently the last segment, the periproct, bearing the anus, never had appendages. Paralleling this, an improvement in the sense organs of the head occurred; eyes and antennae were the ultimate result of

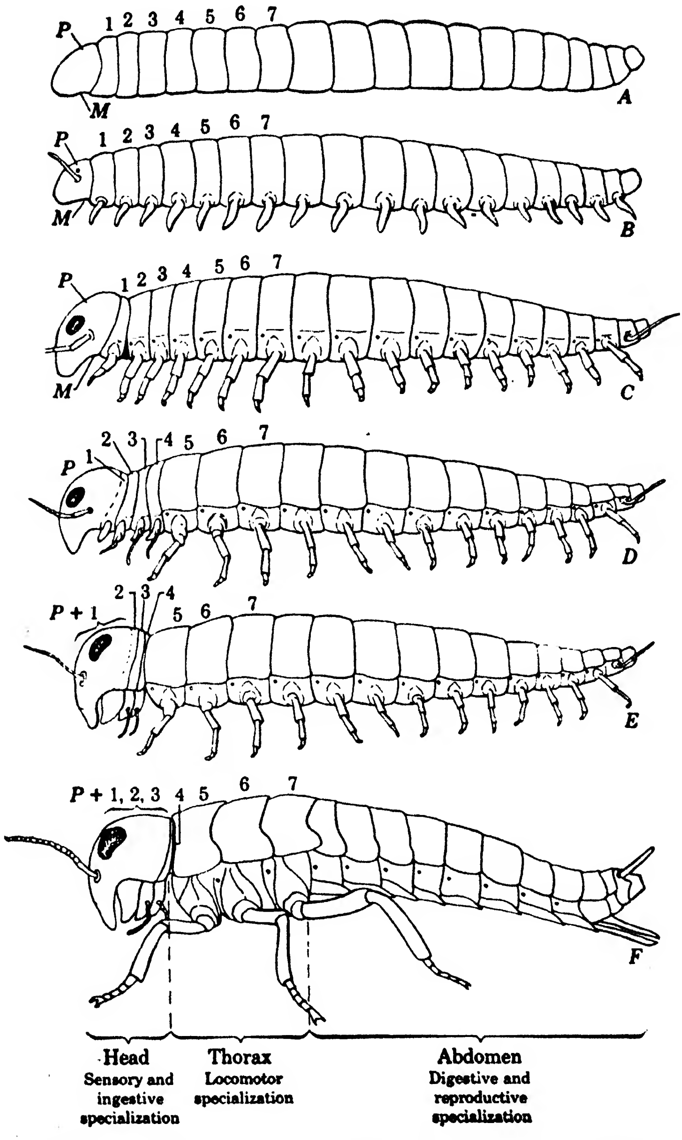

FIG. 13. Diagram showing hypothetical stages (*A* to *F*) in the development of body regions and appendages from a wormlike ancestor to an insect. *M*, mouth; *P*, prostomium. (Modified from Snodgrass)

this. Of the living arthropods, *Peripatus*, fig. 14, is like this phase in regard to development of appendages.

At first the legs were non-segmented. The next step was the development of joints in the legs, a step which would greatly improve their use for locomotion, fig. 13*C*. At about this stage the foremost legs were used for pushing food towards the mouth, rather than for walking. Judging from the condition found in the fossil group Trilobita, it is thought that the first body segment became fused with the prostomium at an early evolutionary stage in order to coordinate better the feeding function of the first pair of legs. Evidence from the same

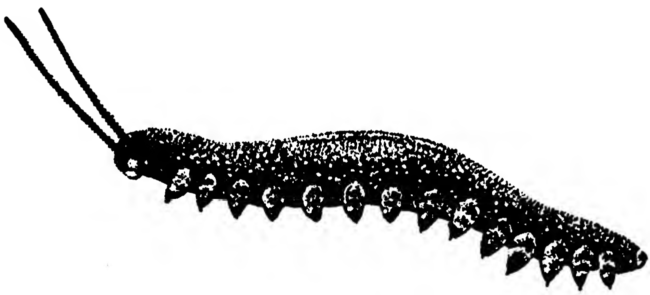

FIG. 14. *Peripatus*. (By permission from MacDougall & Hegner, "Biology: the Science of Life," McGraw-Hill Book Co.)

source indicates that eyes and antennae were well developed at this stage. There are no living arthropods representing such a form as this, but the fossil group Trilobita has essentially this sort of body organization.

At some point near this stage, it appears that the evolving forms of arthropods separated into different paths. One path led to the spider group, fig. 34, and the other led to the mandibulate arthropods which include the insects, centipedes, and crustaceans.

In the branch leading to the insects the next development was the utilization of appendages of segments 2, 3, and 4 as accessory feeding organs, fig. 13*D*. Not only did these appendages push food into the mouth, but also they acquired grinding surfaces to chew and shred the food preparatory to ingestion. Apparently the appendages of the first body segment never developed into strong mouthparts but atrophied in many groups. Appendages of the second body segment ultimately became the mandibles, those of the third became the maxillae, and those of the fourth became the second maxillae or labium. The three segments bearing the mouthparts are termed the *gnathal segments*.

Consolidation of the gnathal segments with the prostomium, fig. 13*E*, resulted in a head structure of compound origin typical of present-day Myriapoda, Insecta, and their allies. This type of head structure is also found in some Crustacea, but in many of these the gnathal segments are not solidly fused with the head, illustrated by the fairy shrimp, fig. 15. This compound structure brings together in one functional unit all the organs intimately connected with feeding. The rest of the body appendages in this stage form a functional unit for locomotion. The classes Pauropoda and Chilopoda (centipedes) are present-day forms showing this type of organization.

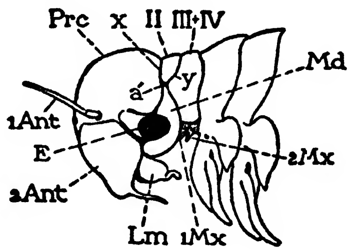

FIG. 15. Head of a fairy shrimp *Eubranchipus*. *a'*, articulation of mandible; *Ant*, antenna; *E*, eye; *Lm*, labrum; *Md*, mandible; *Mx*, maxilla; *Prc*, prostomium plus I; *x*, *y*, sutures of gnathal segments fused with prostomium. (After Snodgrass)

A further body division occurred in the insect branch. The first three pairs of locomotor appendages enlarged; the remainder became reduced and finally disappeared or became modified into non-locomotor structures, fig. 13*F*. This centralized the locomotor function in the first three segments, behind the head, which then formed a well-marked body region, or thorax. The posterior portion of the body containing most of the internal organs is called the abdomen. The posterior appendages of the abdomen became modified as organs for mating or oviposition. Some of the Crustacea have a distinct thorax and abdomen, but in these the thorax is usually composed of about eight segments.

Summarizing these developments from the primitive legless arthropod ancestor, it seems reasonable to suppose that: (1) Similar generalized appendages were developed on all postoral segments, and (2) these were continuously modified and became segregated into groups for specialized functions. In the insects this has resulted in the present distinctive body form composed of three regions: head, with sensory appendages and mouthparts; thorax, bearing three pairs of legs; and abdomen, containing most of the vital organs and having terminal appendages adapted for reproductive functions.

A review of the major groups of the Arthropoda is of interest in visualizing the place of insects among their relatives. In addition, it has a practical application, because the entomologist frequently encounters arthropods other than insects and is called on for information about them. This is especially true of the larger aquatic forms, such as the isopods, and the terrestrial forms that are of economic importance, such as the mites.

TABLE 1. CLASSIFICATION OUTLINE OF THE PHYLUM ARTHROPODA

Class Onycophora—*Peripatus*
Class Trilobita—trilobites (extinct)
Class Crustacea
  Subclass Branchiopoda—fairy shrimps
    Ostracoda—ostracods
    Copepoda—copepods
    Cirripedia—barnacles
    Malacostraca—crabs, shrimps, isopods
Class Arachnoidea
  Subclass Merostomata—king crabs, eurypterids
    Arachnida—scorpions, spiders, mites
    Pycnogonida—sea spiders
    Pentastomida—linguatulids
    Tardigrada—bear animalcules
Class Diplopoda—millipedes
Class Pauropoda—pauropods
Class Chilopoda—centipedes
Class Symphyla—symphylids
Class Insecta—insects

In the following summary of the Arthropoda the emphasis is placed on fresh-water and terrestrial forms, because they usually are found in company with insects. A brief mention is made of marine subclasses to give a complete outline of the major groups. In addition, information is given regarding two fossil groups, the trilobites and the eurypterids, because of their interesting position in arthropod phylogeny.

CLASS ONYCOPHORA

These animals have a wormlike body, indistinctly segmented, each segment except the first and last bearing a pair of ventral non-segmented legs. The anterior segment bears a pair of dorsal antennae and a pair of oral papillae. The mouth opening has a fleshy edge and contains a pair of horny jaws. These curious forms have many characters of the Annelida but are usually considered as archaic arthropods. They feed on humus and are found in moist dark places.

The group is tropical, and occurs in several countries in the neotropical region. Only the single genus *Peripatus,* fig. 14. is known for the class.

CLASS TRILOBITA

The body was divided into head, thorax, and pygidium, the whole usually flattened and divided by two longitudinal furrows into three

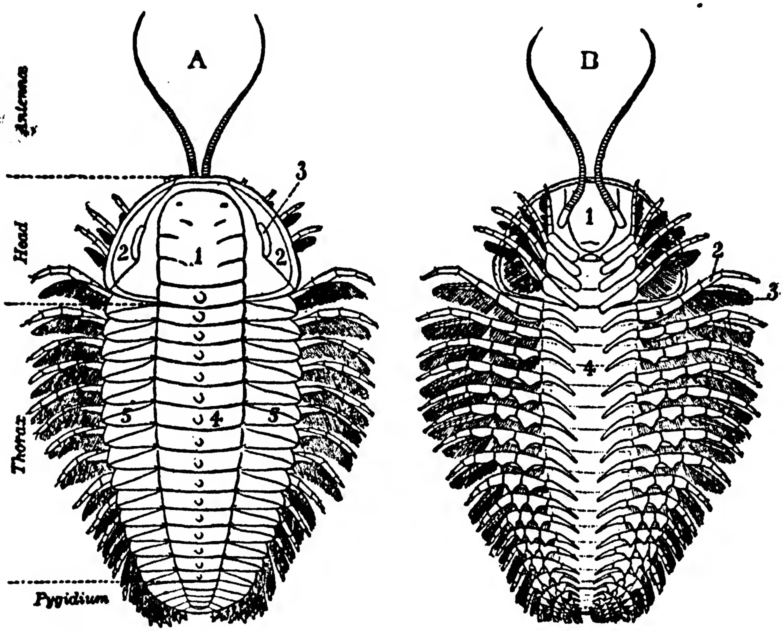

FIG. 16. Sketches of a complete trilobite *Triarthrus becki.* *A,* dorsal or upper side of carapace, showing three lobes, pleura (5), rachis or axis (4), glabella (1), and free cheeks (2) which bear the eyes (3). *B,* ventral or under side, showing biramous limbs (2, 3) attached to rachis, and upper lip or hypostoma (1) which covers mouth. The biramous legs were dual purpose: the upper feathered branch served for breathing gills and swimming paddles, the lower bare branch served for crawling. The short anterior appendages probably aided in feeding. (From Schuchert, after Beecher)

lobes, fig. 16. The head was a loosely organized region consisting of the prostomium (bearing a pair of long segmented antennae) and four body segments each bearing a pair of biramous appendages. Over this structure was a shell-like carapace. Many species had a pair of well-developed eyes. Each segment of the remainder of the body bore a pair of biramous appendages, except for the last segment or telson. In some species, fig. 17, the appendages were uniform throughout the body, and all probably served primarily for locomotion. In others, fig. 16, the appendages of the segments of the head region were shorter than the posterior pairs; it is highly probable that these head appendages were no longer ambulatory in function but served instead to propel food into the mouth.

Trilobites were an abundant marine group in the early Paleozoic era but became extinct at the close of that period. In general actions

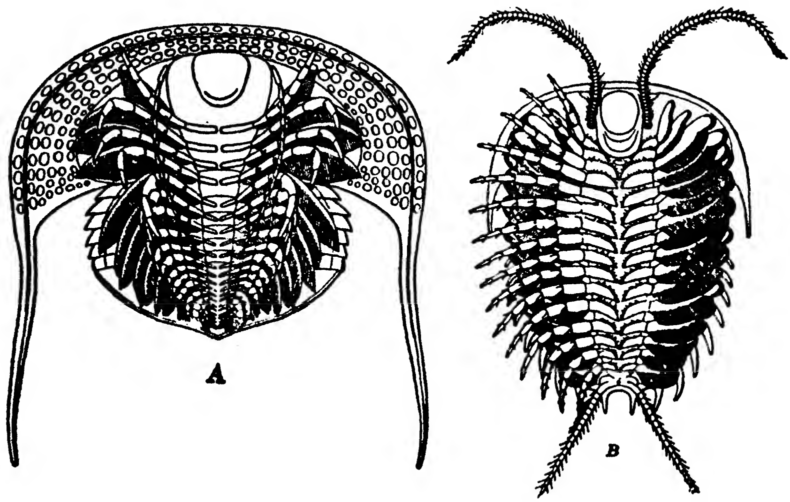

FIG. 17. Restorations of the ventral side of two trilobites, to show the limbs, antennae, and cercopods. *A, Cryptolithus tesselatus,* with the antennae bent back; *B, Neolenus serratus,* with the endopodites omitted on the right side, to show the exopodites better; note the two terminal cercopods. (From Schuchert, after Raymond)

most of them were probably similar to present-day isopods, swimming a little, running over the bottom, and feeding as scavengers. It is thought that some were carnivorous, others were pelagic and lived on plankton, and still others burrowed in the bottom and ingested mud and ooze.

CLASS CRUSTACEA

To this class belongs such a varied assortment of forms that it is difficult to give a brief diagnosis that will apply to all. The majority have the following characteristics: body divided into head, thorax, and abdomen; head and thorax often closely joined and called the cephalothorax; head having two pairs of antennae, a pair of mandibles, and two pairs of maxillae; thorax usually having 4 to 20 distinct segments, each with a pair of segmented appendages; abdomen having one to many segments, with short appendages or none. A few parasitic or sedentary groups have extreme reduction in both body segments and appendages, as in parasitic Copepoda, fig. 25. Several groups have a stout carapace covering much of the body, as in the crayfish, fig. 32; some others have a shell, bivalve in appearance, that incloses most of the body and appendages, fig. 21.

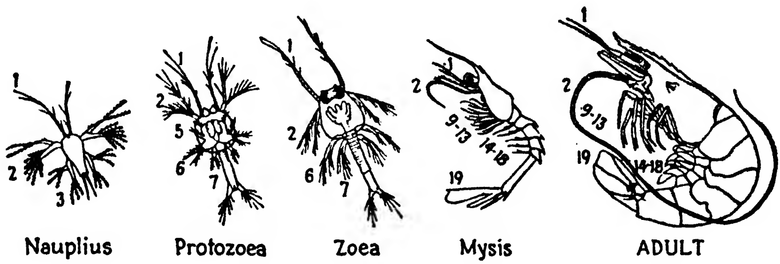

FIG. 18. Metamorphic stages of the shrimp *Penaeus*, showing the succession of changes in body form and in the appendages (1–19). (From Storrer, "General Zoology," McGraw-Hill Book Co., after Müller and Huxley)

Crustaceans rival insects in the variety of diverse forms developed in the class. They share another characteristic with the insects, that in many groups there is a succcession of changes in form in the life history of the individual. In the crustaceans this is well exemplified by the shrimp, fig. 18, which passes through four quite different immature stages before attaining the adult stage, giving a total of five distinctive body forms in the life cycle of the species.

There are five distinct subclasses of Crustacea. Four of these have terrestrial or fresh-water species; the fifth (barnacles) is exclusively marine.

Subclass Branchiopoda, Fairy Shrimps and Water Fleas

This group is characterized chiefly in having the thoracic appendages leaflike and margined with gills. Most of the species live in fresh water.

The true fairy shrimps comprise the order Phyllopoda. Naked (unarmored) forms, fig. 19, are elongate, 10 to 25 mm. long, and swim ventral side up. In central and eastern North America, *Eubranchippus* is a common naked spring form in temporary ponds. Numbers of

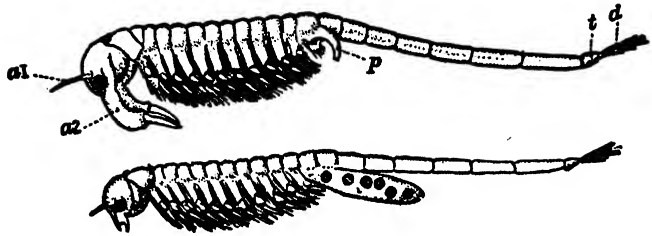

Fig. 19. A naked fairy shrimp *Branchinecta paludosa.* (From Ward & Whipple, after Packard)

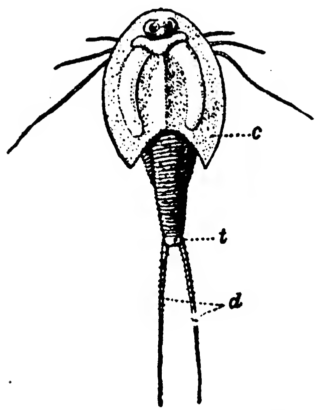

Fig. 20. A shield-bearing fairy shrimp *Apus aequalis.* (From Ward & Whipple, after Packard)

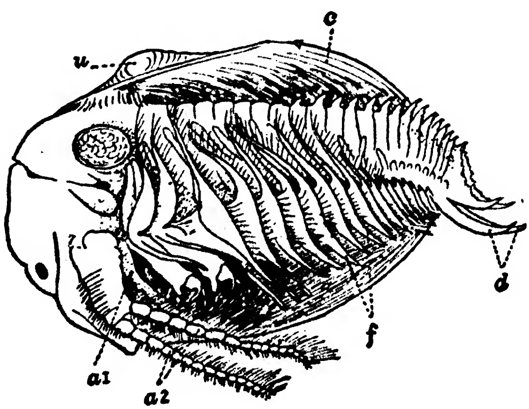

Fig. 21. A bivalve fairy shrimp *Estheria morsei.* (From Ward & Whipple, after Packard)

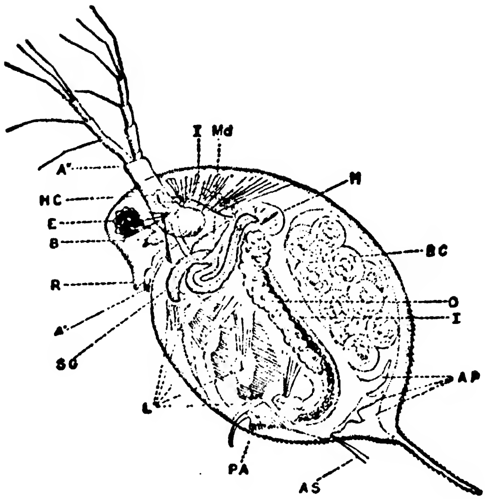

Fig. 22. A bivalve cladoceran *Daphnia longispina*. (From Ward & Whipple, after Birge)

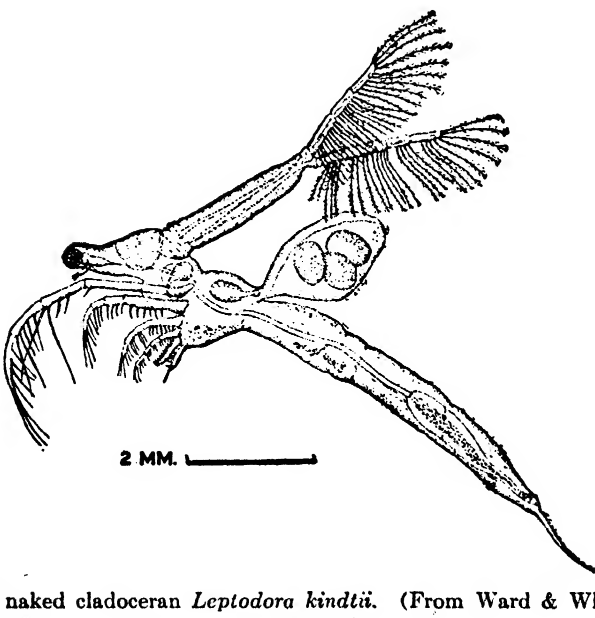

Fig. 23. A naked cladoceran *Leptodora kindtii*. (From Ward & Whipple, after Birge)

these translucent feathery animals swimming about in the cold clear water certainly illustrate why they are called fairy shrimps. In some forms, for example, *Apus,* fig. 20, the dorsum forms a carapace covering head and thorax; others, such as *Estheria,* fig. 21, have a bivalve shell which encloses the entire animal.

The most abundant and widespread branchiopods are the water fleas, the order Cladocera. These are small, averaging about 2 mm. long, and are bilaterally compressed. They have greatly enlarged plumed antennae. Most forms have a bivalve shell, such as *Daphnia,* fig. 22; a few genera have a naked body, as *Leptodora,* fig. 23. The water fleas abound in cool lakes and pools, swimming about with a jerky motion, using the antennae for paddles. The group is an extremely important one from the standpoint of limnological economy.

Subclass Ostracoda, Ostracods

Minute arthropods encased in a bivalve shell, ranging in length from 0.5 to 1.5 mm.; body segmentation indistinct, and having only two pairs of trunk appendages, fig. 24. The group occurs in both salt and fresh water. Fresh-water forms are abundant in North America,

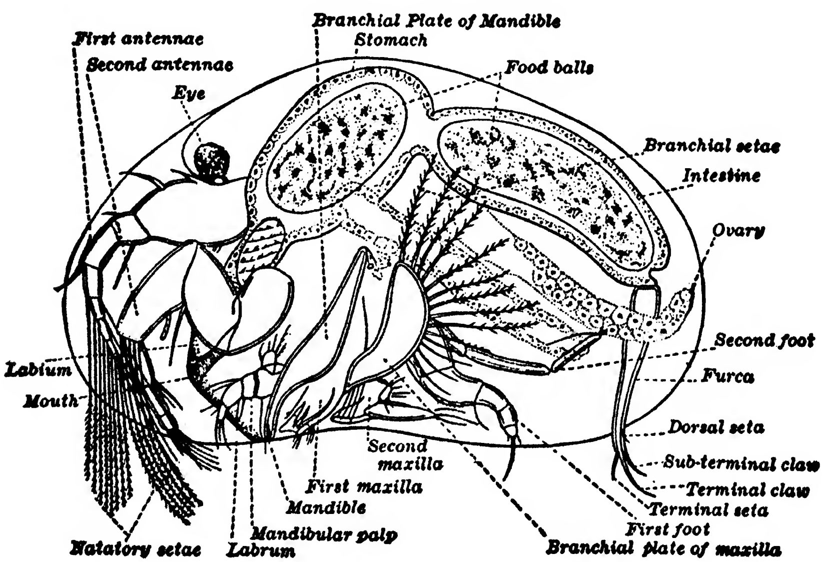

FIG. 24. An ostracod *Cypris virens,* showing general anatomy. (From Ward & Whipple, after Vavra)

occurring in greatest numbers in lakes and both permanent and temporary pools.

Subclass Copepoda, Copepods

Small to minute free-living or parasitic species occurring in fresh or salt water. The North American fresh-water species that are free living have a cylindrical body between 0.5 and 4.0 mm. long, with

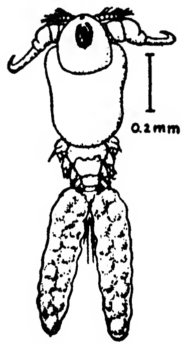

Fig. 25. A degenerate copepod *Ergasilus caeruleus*. (From Ward & Whipple, after Wilson)

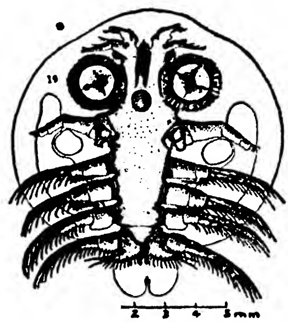

Fig. 26. A complex copepod *Argulus catostomi*. (From Ward & Whipple, after Wilson)

long simple antennae, well-developed mouthparts, four pairs of legs, and a simple posterior body region. They are found along with Cladocera and Ostracoda in a wide variety of aquatic situations. The parasitic species are smaller, most of them about 0.25 mm. long, and attach to fish. There are two types, degenerate forms such as *Ergasilus*, fig. 25, and highly complex forms such as *Argulus*, fig. 26. The former are sedentary parasites, living in gills and nasal passages or boring into internal tissues; the latter attach to the host in more exposed areas, leaving the host at times and swimming about freely.

Subclass Cirripedia, Barnacles

Sessile or parasitic forms of complex highly modified structure, fig. 27. The group is entirely marine in distribution and includes the common barnacle, which does great damage to shore installations and submerged parts of ships.

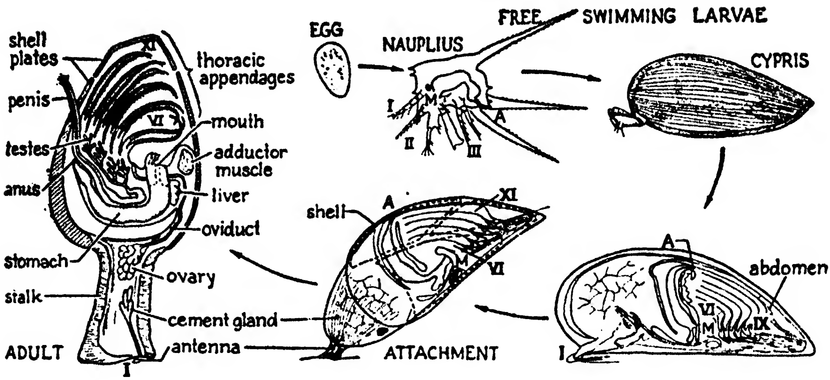

Fig. 27. The goose barnacle *Lepas*. Adult with right side of mantle and shell removed. From the egg a free-swimming nauplius larva hatches, that feeds and molts to become a cypris larva. The latter attaches by its antennules and cement gland and then transforms to the sessile adult stage. Egg and larva much enlarged. *M*, mouth; *A*, anus; I, antennule; II, antenna; III, mandible; VI-XI, other appendages. (From Storrer, "General Zoology," by permission of McGraw-Hill Book Co.)

Subclass Malacostraca, Crabs, Pillbugs, and Their Allies

A varied assemblage of forms ranging in length from a few millimeters to a foot or more. The head bears two pairs of antennae and three pairs of mouthparts; the thorax usually has eight segments, each with a pair of legs, the anterior three pairs sometimes small and serving for accessory mouthparts, called maxillipeds; the abdomen normally has six segments, each with short appendages functioning as gills or reproductive organs. Three of the seven present-day orders are entirely marine; the other four have both marine and terrestrial or fresh-water species.

The isopods, order Isopoda, are dorsoventrally flattened and have no carapace over the thorax, fig. 28. They are scavengers, feeding on decayed organic matter, especially rotten leaves. Fresh-water species are common in swamps, marshes, and small streams. There are several blind species found only in underground water systems. A few small species are terrestrial, known as sowbugs or pillbugs, fig. 28, and live in humid places such as rotten logs and leaf mold, and occasionally are a pest in greenhouses.

Amphipods, comprising the order Amphipoda, have no carapace but are bilaterally compressed and flealike, fig. 29. The fresh-water species are abundant in springs, temporary streams, and lakes, al-

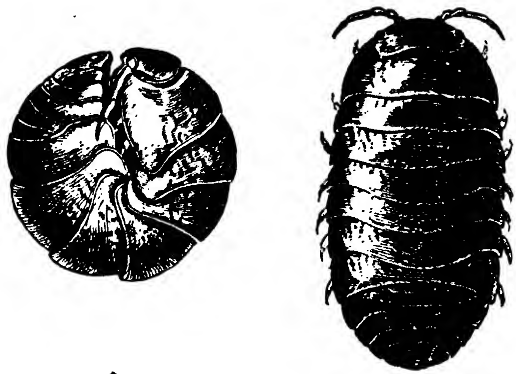

FIG. 28. A terrestrial isopod *Armadillidium vulgare*. Left, in a curled position; right, in walking position. (From U.S.D.A., B.E.P.Q.)

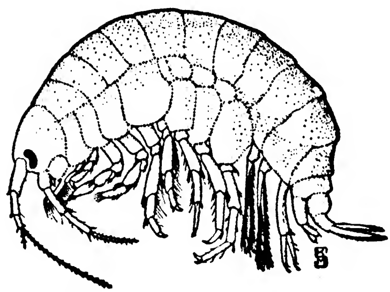

FIG. 29. An amphipod *Gammarus* sp. (From Illinois Natural History Survey)

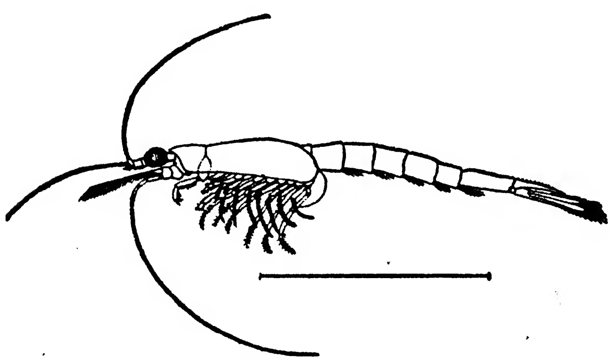

FIG. 30. The only nearctic fresh-water species of the order Mysidacea, *Mysis relicta*. (From Ward & Whipple, after Smith)

though found sparingly in almost all aquatic situations. Like the isopods, the amphipods are scavengers.

Most unusual among fresh-water malacostracans is *Mysis relicta*, fig. 30, the only fresh-water species of the order Mysidacea. It has a carapace that is fused with the first three thoracic segments. The

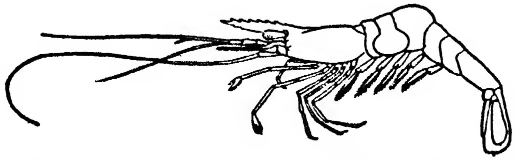

FIG. 31. A fresh-water shrimp *Palaemonetes exilipes*. (From Ward & Whipple, after Smith)

species, though rare, is holarctic in distribution; in North America it is apparently restricted to Lakes Superior and Michigan, into which it probably migrated in glacial times.

The order Decapoda contains our best-known and largest species of fresh-water Crustacea, the shrimps and crayfish. Marine forms

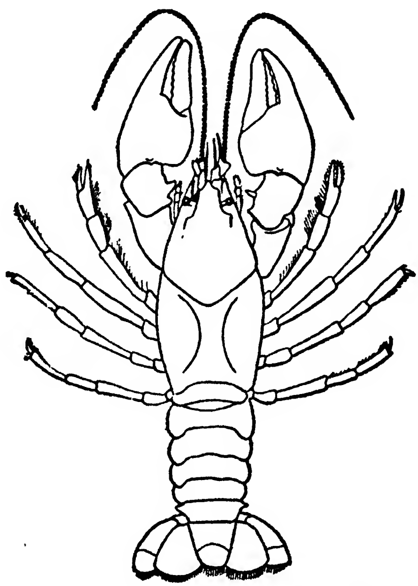

FIG. 32. A crayfish *Cambarus bartoni*. (From Ward & Whipple, after Paulmier)

include the crabs, lobsters, and shrimps. The order is characterized by a well-developed carapace coalesced dorsally with all segments of the thorax. The shrimps, family Palaemonidae, fig. 31, are found in some of the warmer rivers and lakes of the south-central and southeastern states. The crayfish Cambaridae, fig. 32, are common over most of the United States, occurring in a wide variety of aquatic situations. Some species live in low fields, dig burrows down to the water level, and with the excavated material make "chimneys" above the burrow entrance. Crayfish are predaceous or scavengers on small animals.

CLASS ARACHNOIDEA

This class is characterized by the grouping of the anterior segments into a cephalothorax, usually bearing six or eight pairs of segmented appendages, some of the anterior ones modified to form mouthparts. The pair which form the second antennae in the Crustacea is usually modified into a pair of grasping chelicerae or pincers, and the first or prostomial antennae are atrophied. Abdominal appendages are highly modified or lacking. The class is divided into five subclasses, including two of doubtful relationship.

Subclass Merostomata (Gigantostraca)

The abdomen bears pairs of appendages forming gills and platelike coverings; these are used both for respiration and, when the animal

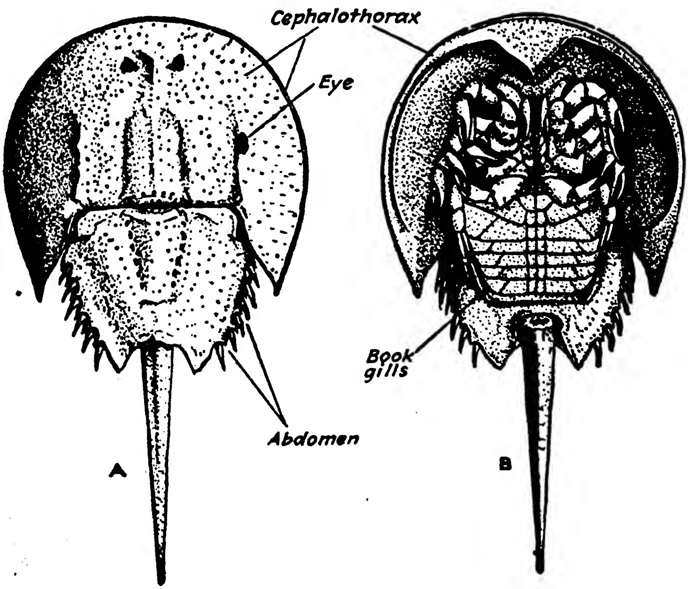

FIG. 33. King or horseshoe crab *Limulus*. *A*, dorsal view; *B*, ventral view. (From Wolcott, "Animal Biology," by permission of McGraw-Hill Book Co.)

is off the bottom, as swimming paddles. The extinct order Eurypterida lacked a carapace and looked somewhat like a scorpion. In the marine order Xiphosura the cephalothorax has a large horseshoe-shaped carapace; the horseshoe crab, *Limulus*, fig. 33, is the only living North American genus of the order.

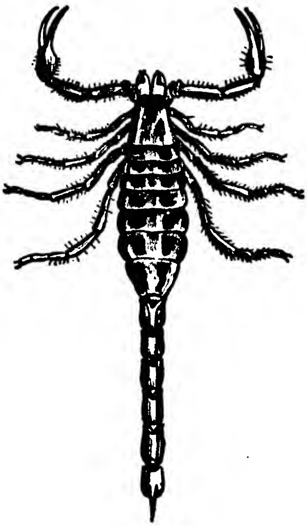

FIG. 34. A scorpion *Buthus carolinianus*. (From Packard, "Guide to the Study of Insects," Henry Holt & Co.)

Subclass Arachnida

The abdomen is large but has no external gills or locomotor organs, and the cephalothorax of the adult bears chelicerae, pedipalps, and four pairs of legs, fig. 34. To this subclass belong the numerous and common living members of the class. Eight orders occur in the United States.

Order SCORPIONIDA

The scorpions, fig. 34, have a segmented abdomen lengthened posteriorly to form a long tail bearing a sting at its tip. The group is a small one confined in North America chiefly to warm dry regions of the Southwest. Scorpions are nocturnal and feed on insects, spiders, and other small animals.

Order PEDIPALPI

These are the whiptail scorpions often called vinegarones. They resemble the scorpions in many respects but lack the sting. The end of the abdomen terminates in a slender whiplike process from which they get their name. This order is also southwestern in distribution.

Order PALPIGRADA

A small group of minute forms about 2.5 mm. long, having an 11-segmented abdomen ending in a 15-segmented tail. The chelicerae are large, but the pedipalps are non-chelate and like the walking legs. Species of this group are known only from the southwestern part of North America.

Order PSEUDOSCORPIONIDA

The pseudoscorpions also resemble scorpions in general shape but lack any vestige of an elongate posterior portion of the abdomen They are predaceous, paralyzing small prey with the pincer-like chelae of the pedipalps, fig. 35. They are found in leaf mold, under bark, in old logs, and sometimes in crevices in houses. In the United States the order is widely distributed, represented by about one hundred species.

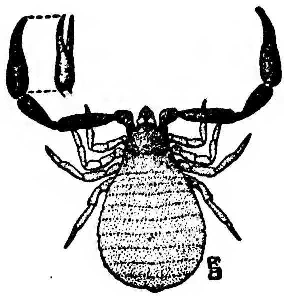

FIG. 35. A pseudoscorpion *Larca granulata*. (From Illinois Natural History Survey)

Order SOLPUGIDA

The solpugids are spider-like in general appearance and in having the pedipalps non-chelate. They are set off from the spiders on the basis of the segmented abdomen which is broad at its base. This is a rare group, the few nearctic species occurring in the Great Plains region and southwestward.

Order PHALANGIDA

The harvestmen, or daddy longlegs, fig. 36, have a broad abdomen, the entire body stout and oval or round in outline; the legs are spindly, frequently five or more times as long as the body. These animals are common in damp shaded woods, where they move about on leaves, tree trunks, and ground, seeking small insects and other food.

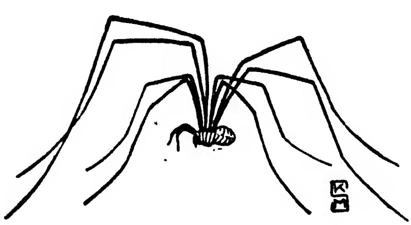

FIG. 36. A harvestman or phalangid. (From Illinois Natural History Survey)

In North America the group is widespread, represented by about two hundred species.

Order ARANEAE

Spiders, fig. 37, are the dominant land group of the Arachnoidea, North America alone supporting several thousand species of them.

Neither legs nor pedipalps are chelicerate; the abdomen shows only traces of segmentation and is constricted at the base to form a thread-waisted joint with the cephalothorax. The pedipalps of the male are highly modified to transfer sperm to the female genital organs; these modifications assume varied shapes and are used extensively in the taxonomy of the group. Spiders are all predaceous on insects and other small animals but aside from this are extremely varied in habits. Some species hunt their prey, running it down or jumping on it; the crab spiders wait in flowers or other places for the prey to come within reach; many groups spin webs in which prey is snared.

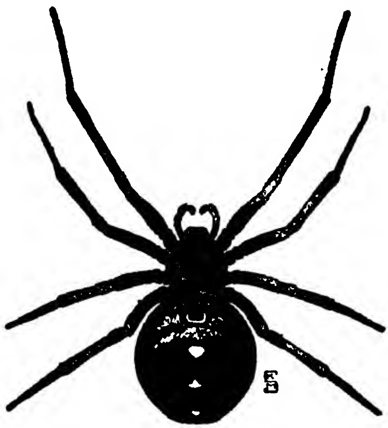

FIG. 37. The black widow spider *Latrodectus mactans*. (From Illinois Natural History Survey)

Order ACARINA

Mites are small in size, ranging from less than 1 to 15 mm. in length, and have the cephalothorax and abdomen fused into a single continuous body region devoid of external segmentation, figs. 38, 39. They are extremely varied in structure and habits. Although there are only a third as many species of mites as spiders, the mites are the most important group economically in the entire Arachnoidea. Several families are ectoparasites of birds and mammals in some or all stages of their life cycles, including ticks (Ixodidae), fig. 38, chiggers (Trombiculidae), mange or itch mites (Sarcoptidae), and follicle mites (Demodicidae). Species of "red spiders" (Tetranychidae), fig. 39, attack leaves and cause defoliation of many crops. Various Tyroglyphidae, bulb mites, attack stored products and bulbs and roots of bulb crops.

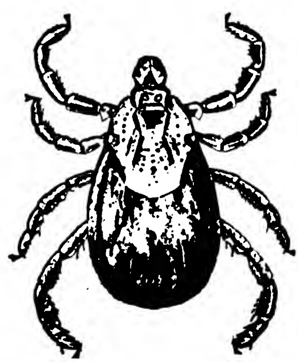

FIG. 38. The eastern dog tick *Dermacentor variabilis*. This is one of the vectors of Rocky Mountain spotted fever. (From U.S.D.A., B.E.P.Q.)

Members of the family Eriophyidae produce blisters and galls on several commercial crops, notably pears. One family, the Hydrachnidae,

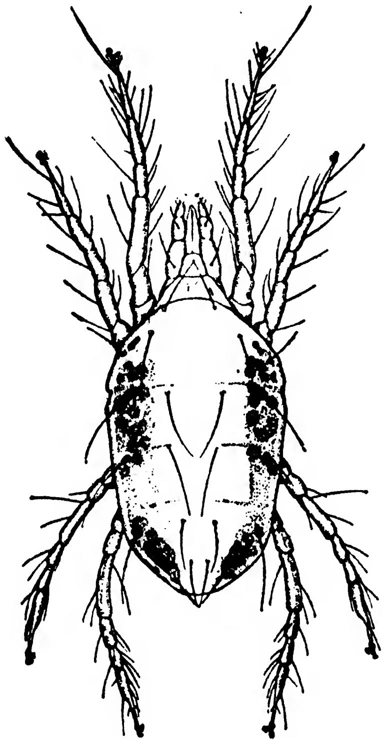

FIG. 39. A red spider *Tetranychus bimaculatus,* really a mite and not a spider. This mite is greatly enlarged; actually it is much smaller than the tick shown in fig. 38. (From U.S.D.A., B.E.P.Q.)

is aquatic, found in a wide variety of fresh-water habitats. In addition to economic species, there are many others occurring in soil and ground cover and as ectoparasites on many native birds and mammals.

Subclass Pycnogonida

This contains the sea spiders, fig. 40, a small marine group of spider-like forms having a minute peglike abdomen. Sea spiders are found mostly on hydroids and sea anemones, but occasionally on jellyfish.

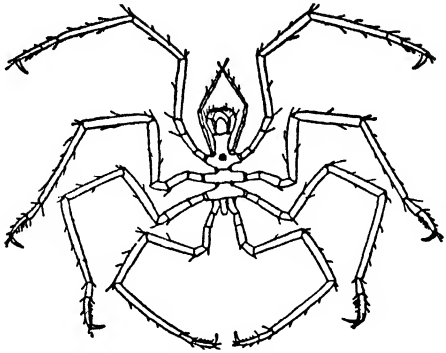

FIG. 40. A pycnogonid *Nymphon.* (From U.S.D.A., B.E.P.Q.)

Subclass Pentastomida (Linguatulida)

In this small group are placed endoparasites, fig. 41, having a much-reduced wormlike adult structure, but having a four-legged larva

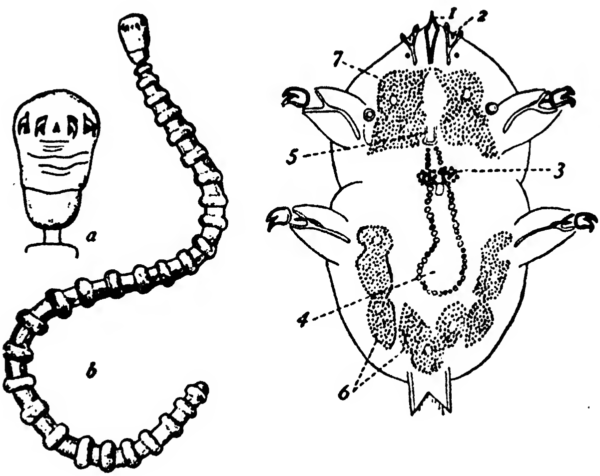

FIG. 41. A linguatulid. Left, *Porocephalus annulatus; a,* ventral view of head; *b,* ventral view of entire animal. Right, larva of *Porocephalus proboscideus,* ventral view; 1, boring anterior end; 2, first pair of sclerotized processes seen between the forks of the second pair; 3, ventral nerve ganglion; 4, alimentary canal; 5, mouth; 6 and 7, gland cells. (After Stiles and Shipley)

resembling to some extent the larvae of mites. The exact relationship of the group is doubtful, but many authors place it tentatively in the Arachnoidea on the basis of larval structure. The various species parasitize a variety of vertebrates.

Subclass Tardigrada

The water bears or tardigrades, fig. 42, are minute animals that live in wet moss and in both fresh and salt water. The body, never more than a millimeter long, has four pairs of legs terminating in claws; the head has neither apparent mouthparts nor other appendages.

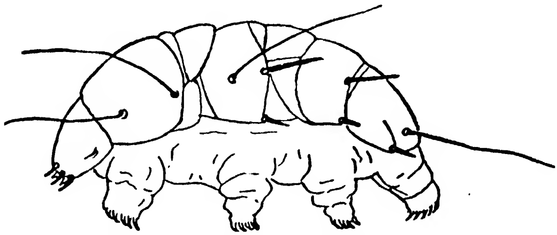

Fig. 42. A tardigrade. (After U.S.D.A., B.E.P.Q.)

The affinities of this group are unknown; it may be entirely unrelated to the Arachnoidea but because of its four pairs of legs is placed here on a tentative basis.

Myriapod Group

Four classes, the Diplopoda, Chilopoda, Symphyla, and Pauropoda, have centipede-like shapes and are often termed the myriapods. They all have a distinct head (composed of the original prostomium fused with several body segments whose appendages form the mouthparts) and an elongate trunk region bearing segmental ambulatory or walking legs. In each of these four classes the antennae are present, sometimes well developed. Although these classes share many superficial resemblances, differences in basic structure indicate that they are quite widely separated phylogenetically.

CLASS DIPLOPODA

This includes the millipedes or thousand-legged worms, fig. 43. The body segments have fused into pairs, so that each apparent segment has two pairs of legs. The mouthparts consist of two pairs of appendages, fig. 44, a pair of mandibles at least superficially resembling those of insects, and a platelike

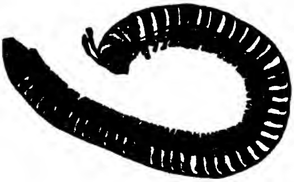

Fig. 43. A diplopod or millipede *Parajulus impressus*. (From Illinois Natural History Survey)

gnathochilarium composed of a fused pair of appendages and resembling the insectan labium in general appearance. The reproductive organs open behind the second pair of legs.

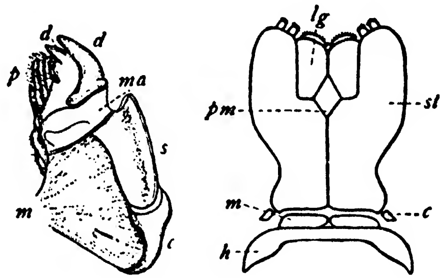

FIG. 44. Mouthparts of a diplopod *Julus*. Left, mandible; *c*, cardo; *d*, teeth; *m*, muscle; *ma*, mala; *p*, pectinate plate; *s*, stipes (after Latzel). Right, gnathochilarium or second jaws; *c*, cardo; *h*, hypostoma; *lg*, linguae; *m*, mentum; *pm*, promentum; *st*, stipes. (After Silvestri)

Millipedes live in leaf mold, rotten logs, and other humid places. About one hundred species occur in the United States, especially in forested localities. A few species feed on living plants and become of local economic importance.

CLASS PAUROPODA

A few genera of minute animals, fig. 45, centipede-like in shape, comprise this class. The body consists of 12 segments, of which the dorsal portions are fused in pairs; nine segments each bear a pair of legs, each pair evenly spaced from the next. The antennae are biramous, unlike any of their relatives. Eyes are represented by only a small spot. The mouthparts, fig. 46, consist of two pairs of jaws and a curious complex lower lip. As in the Diplopoda, the reproductive organs open in the anterior part of the body.

The few North American species are a millimeter or two long and live in moist ground cover, probably feeding on humus. The genus *Pauropus* has a slender white body, and looks like a small centipede, fig. 45. The genus *Eurypauropus* is short and stout, covered with scales, and looks like a minute sowbug (isopod) fig. 47. Both genera are taken occasionally in ground-cover samples in the eastern half of the United States.

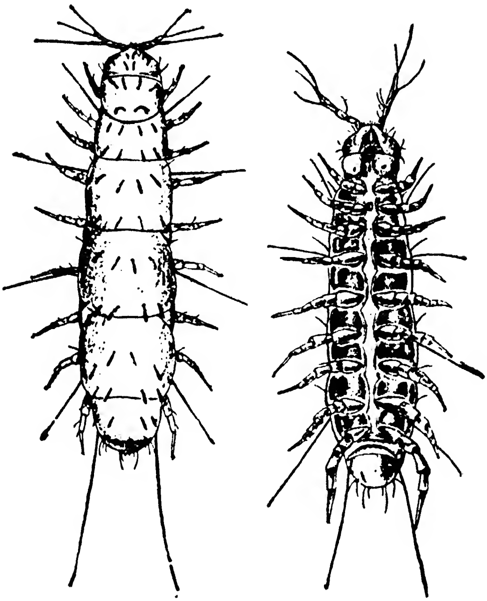

FIG. 45. A pauropod *Pauropus huxleyi;* left, dorsal aspect; right, ventral aspect (After Kenyon)

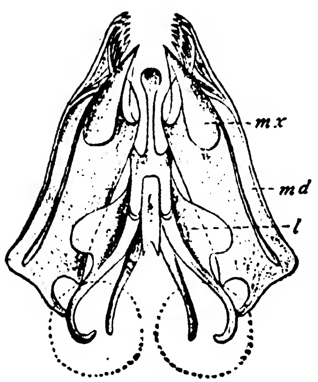

FIG. 46. Mouthparts of a pauropod *Eurypauropus ornatus.* *md,* mandible; *mx,* second jaws; *l,* lower lip. (After Latzel)

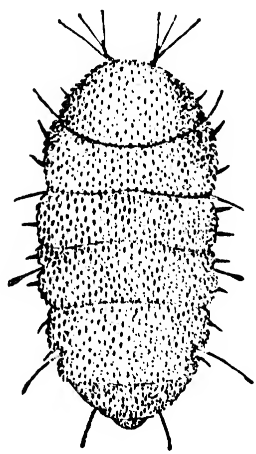

FIG. 47. A sowbug-like pauropod *Eurypauropus spinosus.* (After Kenyon)

CLASS CHILOPODA

Here belong the centipedes, fig. 48. They are elongate and many-segmented, with a pair of legs on each segment, and with the reproductive openings on the penultimate body segment. The head bears

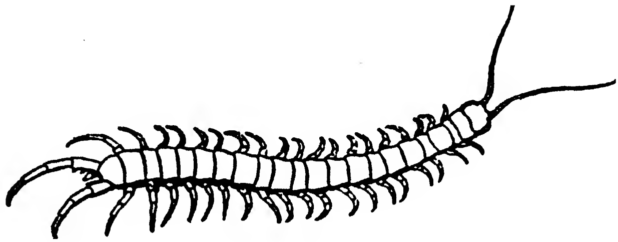

FIG. 48. A typical centipede. (After Snodgrass)

long antennae and has eyes which are either compound or composed of single facets. The mouthparts, fig. 49, consist of three pairs of appendages: the jawlike mandibles; the maxillae, which are fused and resemble the insect labium; and the second maxillae or palpognaths, which are leglike, sometimes with the coxae fused. An interesting fea-

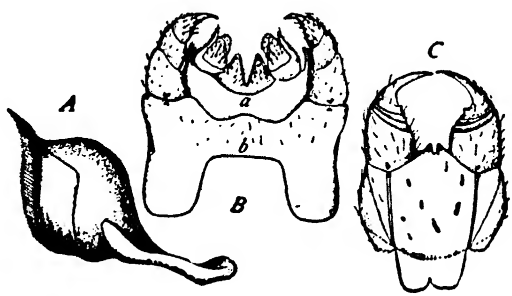

FIG. 49. Mouthparts and poison jaws of a centipede *Geophilus flavidus*. *A*, right mandible. *B*, the two pairs of maxillae; *a*, the united coxae of the first maxillae; *b*, the united coxae of the second pair or palpognaths. *C*, the poison claws or toxicognaths. (After Latzel)

ture of the Chilopoda are the poison claws, fig. 49. These are appendages of the first trunk segment but are held beneath the head and superficially resemble mouthparts.

Chilopoda are predaceous in habits. About one hundred species are known from the United States. Most of them are nocturnal, moving about only at night in search of prey and hiding during the day in leaf mold, rotten logs, and galleries in soil. Species in temperate climates seldom exceed 1½ inches in length, but in the extreme southern United States occur a few tropical species 8 or 10 inches long. One species having especially long legs is common in houses, fig. 50.

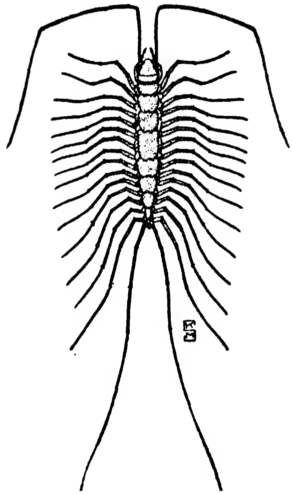

FIG. 50. The house centipede *Scutigera forceps*. (From Illinois Natural History Survey)

CLASS SYMPHYLA

Members of this class are about ¼ inch long and centipede-like in form, fig. 51, and have the trunk composed of about 15 segments (none fused in pairs) of which 11 or 12 bear legs. The reproductive openings are at the posterior end of the body. The head is remarkably insectan in many characters: it possesses an epicranial stem and long antennae, and the mouthparts, fig. 52, consist of mandibles, maxillae, and labium. For these reasons the Symphyla are considered as the closest relatives of insects. Members of the group are rare, usually occurring in humus. Occasionally they are a pest in greenhouse benches, eating the roots of plants. In the United States the genus *Scolopendrella* is sometimes found in ground-cover samples. On cursory examination, small individuals may be confused with Pauropoda, which occur in the same type of situation.

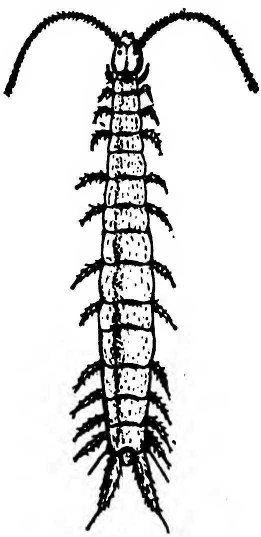

FIG. 51. A symphylid of the genus *Scolopendrella*. (After Latzel)

CLASS INSECTA—THE INSECTS

All insects belong to this class. They are distinguished primarily by having six legs, a pair on each segment of the thorax. From this condition comes the term Hexapoda, meaning six-legged, which is sometimes used as the class name for insects.

Characteristics

A typical adult insect has three body regions, fig. 53. The anterior region is the head, which bears eyes, antennae, and three pairs of mouthparts. The next region is the thorax which is composed of three segments, each usually bearing a pair of legs; in many groups the second and third segments each bear a pair of wings. The posterior portion of the body is the abdomen. It consists of as many as 11 segments and has no legs. The eighth, ninth, and tenth segments usually have appendages modified for mating activities or egg laying.

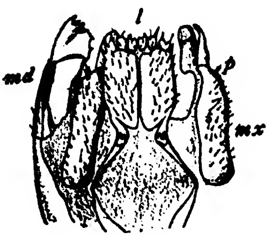

FIG. 52. Mouthparts of *Scolopendrella*, ventral aspect. *md*, mandible; *mx*, maxilla; *s*, stipes; *p*, palpus; *l*, second maxillae or labium. The mandible on the right side of the figure is omitted. (After Hansen)

The exoskeleton in insects, as in other arthropods, provides both the protection for the vital organs and the support which maintains the body shape. The chief internal organs consist of the following parts: (1) a tubular digestive tract; (2) a long valvular heart for pumping the blood; (3) a system of pipelike tracheae for respiration; (4) paired reproductive organs opening at the posterior end of the body; (5) an intricate muscular system; and (6) a nervous system consisting of a brain, paired segmental ganglia, and connectives.

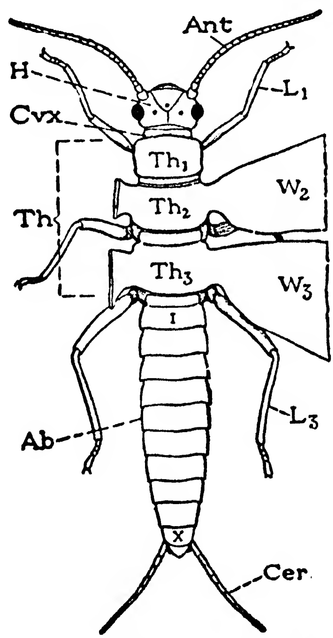

FIG. 53. Diagram of an insect. *Ab*, abdomen; *Ant*, antenna; *Cvx*, cervix; *Cer*, cercus; *H*, head; *L*, leg; *Th*, thorax; *W*, wing. (After Snodgrass)

Immature insects do not have wings. The only known exception to this is found in the order Ephemeroptera, mayflies, in which the last brief immature instar has functional wings. Immature insects may be entirely unlike their adults in general appearance and may lack legs, a definite head, and many other structures typical not only of insects but also of other arthropods.

The orders of insects are outlined in Table 2 and described in Chapter 7.

TABLE 2. CLASSIFICATION OUTLINE OF INSECT ORDERS

Subclass Oligoentoma—order Collembola—springtails.
Subclass Myrientomata—order Protura—proturans.
Subclass Euentomata—typical insects:
- *A*. Apterygota—primitive wingless orders:
  - Order Thysanura—silverfish.
    - Diplura—campodeans and japygids.
- *B*. Pterygota—winged insects:
  - (*a*) Hemimetabola—insects with gradual metamorphosis:
    - Order Ephemeroptera—mayflies.
      - Odonata—dragonflies and damselflies.
      - Orthoptera—cockroaches, grasshoppers.
      - Dermaptera—earwigs.
      - Plecoptera—stoneflies.
      - Diploglossata—hemimerids.
      - Isoptera—termites.
      - Zoraptera—zorapterans.
      - Embioptera—embiids.
      - Corrodentia—psocids.
      - Mallophaga—chewing lice.
      - Thysanoptera—thrips.
      - Anoplura—sucking lice.
      - Hemiptera—bugs (Heteroptera and Homoptera).
  - (*b*) Holometabola—insects with complete metamorphosis:
    - Order Neuroptera—lacewings.
      - Megaloptera—dobsonflies.
      - Mecoptera—scorpionflies.
      - Raphidiodea—snake-necked flies.
      - Hymenoptera—bees, ants, and wasps.
      - Coleoptera—beetles.
      - Trichoptera—caddisflies.
      - Lepidoptera—butterflies and moths.
      - Diptera—two-winged flies and mosquitoes.
      - Siphonaptera—fleas.

Success as a Group

Insects have attained the largest number of kinds of any animal group, with an estimated million or more species; sometimes they occur in such numbers as to swarm in dark clouds or, attracted to lights, blanket the streets of a city a foot or more deep with their bodies.

In competition with other animals they have been able to fit into and populate almost every nook and cranny of the globe except the depths of the ocean. They abound throughout the tropics and also are one of the very few permanent animal inhabitants of the South Polar Region; aquatic insects may practically pave the bottom of large rivers and lakes and also develop to maturity in the water in hoofprints; in one case grasshoppers may range over miles of prairie, in another a brood of maggots may feed and mature within a single rotting walnut husk, and in still another case a wasp may mature within the tiny seed of a small plant.

TABLE 3. ESTIMATED NUMBER OF LIVING ANIMAL SPECIES KNOWN AT PRESENT FOR THE WORLD

Group	*Number of Species*
Chordata	38,000
Arthropoda exclusive of insects	50,000
Insecta	900,000
Mollusca	80,000
Echinodermata	5,000
Annelida	5,000
Molluscoidea	2,500
Platyhelminthes	6,500
Nemathelminthes	3,500
Trochelminthes	1,500
Coelenterata	5,000
Porifera	3,000
Protozoa	15,000
Total	1,115,000

These are but a few fragments of the evidence that insects are a remarkably successful group of organisms. With this in mind it is interesting to speculate on some of the reasons why they have developed to such huge numbers of both species and individuals.

Adaptive Features

Among arthropods, insects represent the culmination of evolutionary development in terrestrial forms. They have exploited the mechanical advantages of an exoskeleton and used them as a basis on which to add specializations which give them still further advantages over their competitors. Chief advantages of an exoskeleton include (1) a large area for internal muscle attachment; (2) an excellent possibility of evaporation control, especially in small-bodied animals; and (3) almost complete protection of vital organs from external injury.

To this foundation insects have added other specializations, some morphological and some physiological, which have been a decided factor in assisting them to attain their present development. The more outstanding of these specializations are enumerated in the following paragraphs.

Functional Wings. The power of flight greatly increased the statistical chances of survival and dispersal, except on wind-swept islands. It increased feeding and breeding range and provided a new means of eluding enemies. Increased feeding range undoubtedly opened the way for adoption of foods of more specific limitation, especially in those cases in which the host or breeding medium occurred in small quantities and scattered situations. For example, it would allow a species to adopt carrion as a food, since the individual with functional wings could seek out and reach carcasses which would be not only isolated but also suitable as food for only a short period.

Small Size. In the main, insect evolution has followed the course of developing many small individuals rather than fewer large ones. This has made available many new specific foods occurring in small quantity and has increased chances of hiding from and eluding enemies. Small size has this disadvantage, that the total body surface increases tremendously in proportion to the body volume. This results in a high evaporation quotient which would make terrestrial life impossible for a thin-skinned animal. The exoskeleton of insects has provided a check to this evaporation quotient, and the possession of this exoskeleton is undoubtedly one of the principal factors which have allowed insects to develop small size.

Adaptability of Structures. Insects have adapted the same structure to perform different functions. For instance, the front legs of mantids and ambush bugs grasp and hold prey while it is being devoured, thus functioning as accessory mouthparts, rather than as ambulatory legs. Insects have also adapted the same structure to function under entirely different conditions, for example, the diverse modifications of the respiratory system, which has been adapted for many types of both aquatic and terrestrial life.

Complete Metamorphosis. This development among certain groups of insects is unique in the animal kingdom. It is a specialization in which the life history is divided into four distinct parts, (1) the egg, (2) the larva or feeding stage; (3) the pupa, a quiescent transformation stage, and (4) the adult or reproductive stage. In this type of life history all real growth is the result of larval feeding; the adult has only to maintain a more or less static metabolism and at the most provide sufficient food for maturation of sperms or eggs. This system has enabled the larva and adult to live in entirely different places and under different conditions, so that the larva has been able to take advantage of conditions most favorable for rapid growth and the adult to live in conditions best suited to fertilization, dispersal, and oviposition. Complete metamorphosis opened to the group an infinite variety of habitat and food possibilities. In connection with it there has often been a varied development of complex instinctive behavior. In addition, extremely short life cycles have frequently been developed, based on the extraordinary feeding and digestive ability of some of the larvae; a flesh-fly maggot, for instance, can develop from hatching to a full-grown larva in 3 days. In short, complete metamorphosis has enabled a species to combine the advantages of two entirely different ways of life and at the same time avoid many of the disadvantages of both.

High Fecundity. Although this condition is the rule rather than the exception among lower animals, it should not be overlooked as a factor contributing to insects' success.

Individual queens of termites and some other social insects may lay as many as several hundred thousand eggs. Mayflies and some parasitic flies deposit several thousand eggs each; many moths, flies, stoneflies, and representatives of other orders deposit in the magnitude of hundreds of eggs per female. On the other extreme are the oviparous females of certain aphids, which produce only one egg each, but this is compensated for by high fecundity of other generations in the same species.

No one factor of these can be considered the most important reason why insects have achieved their present diversity and numbers. The process has been most complex, with various combinations of these factors and undoubtedly others working together to produce the end result. It should be borne in mind that not every insect has made use of every one of these specializations. For example, entire orders of insects, such as the chewing lice, sucking lice, and fleas, have lost all trace of wings, correlated with a limited sphere of activity on or near the host. Complete metamorphosis does not occur in about half the orders, but in these other features come into play. It must be remembered, too, that these specializations are only a few of the most important of the very large number that have been developed in the class Insecta.

Adaptability

Perhaps the most outstanding and unexpected circumstance about the situation is that individuals and individual species of insects have practically no adaptability. The adaptability of the insect group as a whole has been due to the development of innumerable species, each adapted for a specialized existence and abode. For instance, many species feed on only one species of plant; if the supply of that one plant species becomes exhausted, the insects cannot complete development on any other kind of plant. On the other hand, there are so many species of plant-feeding insects that practically no species of plant is immune from their attack, and some plants, such as the oaks, may support several hundred different insect species. Most insects, at least during some phase of their development, require extremely critical combinations of temperature and humidity. There are so many insect species, however, each with different requirements, that one or more species seem to occur in every conceivable situation from the tropics to the polar regions, from the desert to the rain forest, on land and in water.

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3

External Anatomy

This chapter deals primarily with the external parts and divisions of the body and its appendages. Before proceeding to the description of these parts, it is necessary to understand a few generalities regarding the body wall, from which the parts are formed.

BODY WALL AND EXOSKELETON

The body wall of insects serves as an exoskeleton and is the only counterpart in insects to the internal skeleton of vertebrates. To the exoskeleton are attached the principal muscles which give the body cohesion. The body wall may have considerable spring or flexibility, but, except for a short time after a molt, *it will not stretch.*

In order to gain both protection and a rigid attachment spot for muscles, various parts of the body wall have become hardened or sclerotized. Now, if all the body wall were uniformly hard, there would be no possibility of movement, whether for purposes of locomotion or for expansion to accommodate important activities such as food ingestion or development of eggs. To overcome this difficulty, the hardened body areas form a series of plates, or *sclerites,* between which the body wall is soft and flexible, or membranous. This arrangement permits the development of hard exterior plates for protection and rigidity and at the same time allows many types of movement.

A simple example of how this works is found in the abdomen of the mosquito, fig. 54. When the abdomen is not engorged, a cross section of the body wall of the abdomen is narrow and elliptic, fig. 54*A;* the dorsal plate and ventral plate are connected at the sides by a strip of membrane which is very finely accordion-pleated. As the abdomen enlarges during a blood meal, these membranes simply unfold, allowing the dorsal and ventral plates to be pushed farther apart by the increasing volume of food being pumped into the abdomen. At its greatest expansion, the body cross section is nearly circular, fig. 54*B*.

Another common type of membranous connection, shown in fig. 55, works on the principle of telescoping rings. When the membrane is

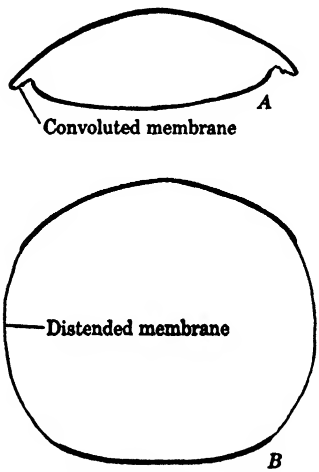

Fig. 54. Cross section of mosquito abdomen, diagrammatic. *A*, contracted; *B*, expanded.

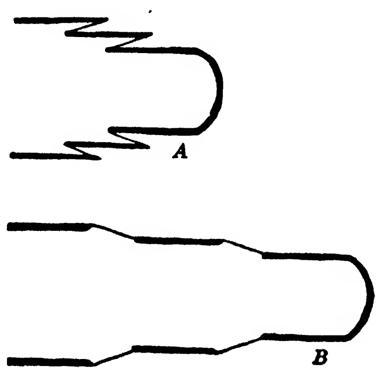

Fig. 55. Medial section of telescoping ring segments, diagrammatic. *A*, retracted; *B*, extended. The thin portion represents membrane.

retracted, as in *A*, the rings overlap, and the membrane is drawn in with the telescoped section. When it is extended, as in *B*, the sections may be pushed out to the limit of the length of their connecting membrane.

Figure 56 illustrates how a flexible membranous strip affords articulation of a leg joint. To the right, a narrow strip of membrane forms a hinge between the leg and one plate; to the left a roll of membrane connects the leg and the other plate. In *A* the leg is held straight out; note that the left membrane forms a series of pleats. In *B* the appendage has been pulled forward; to accommodate this, the left membrane has simply stretched out as the corner of the leg moved inward and back.

A common type of articulation found at leg joints of adult insects is illustrated in fig. 57. When the segment to the right is extended, as in *A*, the upper membrane *u* is folded, and the lower membrane *l* is stretched out. When the segment is pulled down, as in *B*, the upper membrane is pulled out, and the lower membrane is folded or pleated.

In all four of these examples movement has been made possible by flexibility, not elasticity. The illustrations do not show the muscles

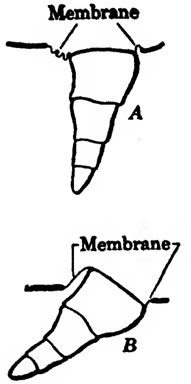

FIG. 56. Articulation of a membranous leg joint. *A*, held straight out; *B*, pulled forward.

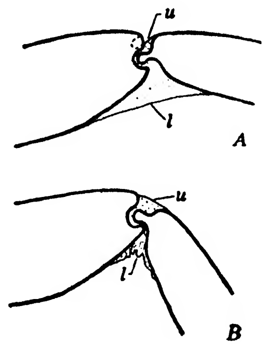

FIG. 57. Membranous connections of a ball-and-socket leg joint. *A*, held straight out; *B*, pulled in. *u*, upper membrane; *l*, lower membrane.

which actually *cause* the movements, but only the membranous connections which *permit* movement.

Sclerites. The hardened or sclerotized areas of the body are called sclerites. The major sclerites are usually separated by areas or lines of membrane. Many major sclerites may be subdivided by furrows or new lines of membrane into additional sclerites. Sclerites may also unite, usually with an evident line, furrow, or seam along the line of fusion. In entomological usage these types of demarcation—membrane strips, furrows, and fusion lines—are called sutures. The term sclerite is applied loosely to any sclerotized surface area, bounded by sutures of any type.

External Processes. The surface of the integument usually bears many kinds of processes, including wrinkles, spurs, scales, spines, and hair. These are outgrowths of the body wall. They are of only incidental interest to the general subject of external anatomy but are extremely important as taxonomic characters in many groups of insects.

Internal Processes. There are many processes which are formed by the invagination of the body wall. These are called *apodemes.* Their point or line of invagination is almost always indicated by an external pit or groove. These pits and grooves provide some of the most reliable landmarks for identifying their parent sclerites. The apodemes provide internal areas for muscle attachment.

BODY REGIONS

The adult insect body is divided into three parts: the head, thorax, and abdomen. The phylogenetic origin of these regions is discussed on page 26. The head is usually a solidly constructed capsule no longer having distinct segmentation. The thorax and abdomen have both preserved distinct segments of more or less ringlike form.

Legless immature instars of some insects have little differentiation between body regions. The head is usually distinct, but the segments of both thorax and abdomen may be identical in appearance and form a single uniform body region, the trunk.

Orientation. In describing the relative position or various parts of an insect, several sets of terms are used to indicate direction or position. Certain body regions are used as a basis for orientation, chiefly the following:

1. Anterior portion, the portion of the body bearing the head; or that portion of any part that is toward the head end.

2. Posterior portion, the portion of the body bearing the cauda, or "tail end" of the abdomen; or that portion of any part that is toward the posterior end.

3. Dorsum, the top or upper side of the body or one of its parts.

4. Venter, the underside or lower side of the body or one of its parts.

5. Meson, the longitudinal center line of the body, projected on either the dorsal or ventral aspect, or any point in between.

6. Lateral portion, the side portion of the body or one of its parts.

7. Base, apex; in appendages or outgrowths of the body, such as antennae or legs, the point or area of attachment is called the base; the tip or furthermost point from the attachment is called the apex. In parts of appendages, such as a segment of a leg, the same orientation is used; the part articulated nearest the body is the base or proximal portion; the part away from the body is the apex or distal portion.

THE HEAD

The head, fig. 58, comprises the anterior body region of an insect. It is normally a capsule with a sclerotized upper portion, which con-

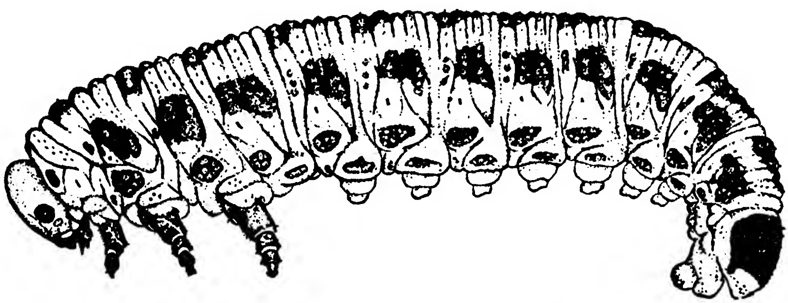

Fig. 58. Sawfly larva *Neodiprion lecontei,* illustrating a hypognathous head. (After Middleton)

tains the brain, and a membranous floor, in which is situated the oral opening or mouth.

Origin. The head is a composite structure consisting of the primitive prostomium to which have fused the first four postoral segments. So complete is this fusion that there remains little evidence to indicate this origin of parts. The only definite intersegmental suture still distinct is the postoccipital suture, which marks the division between the third and fourth postoral segments.

Position. The head may assume various positions in relation to the long axis of the body. These positions are frequently used in classification. The two most important positions have been given definite names:

Hypognathous: the mouthparts are directed downward, and the head "segments" are in the same position as the trunk segments, fig. 58. This is the generalized condition.

Prognathous: the head is tilted up at the neck so that the mouthparts project forward, fig. 59.

Head Organization and Appendages. In a typical hypognathous head, fig. 60, the anterior region or face, the dorsal portion, and lateral portion form a continuous sclerotized capsule which is open beneath, like an inverted bowl. On this capsule are situated a pair of compound eyes, three ocelli, and a pair of antennae. The labrum hangs

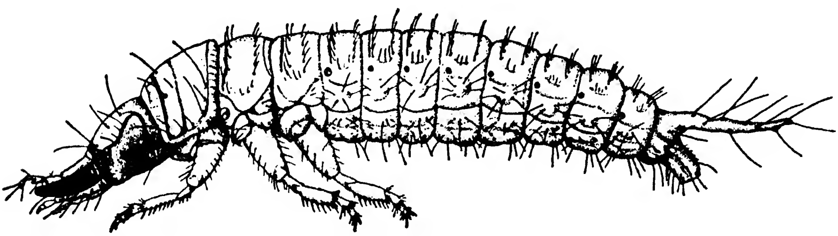

Fig. 59. Ground beetle larva *Harpalus pennsylvanicus*, illustrating a prognathous head. (From Illinois Natural History Survey)

down from the lower front margin of the capsule to form a flap in front of the mouth. The ventral portion of the head forms a membranous floor posterior to the mouth; from this floor arises the hypo-

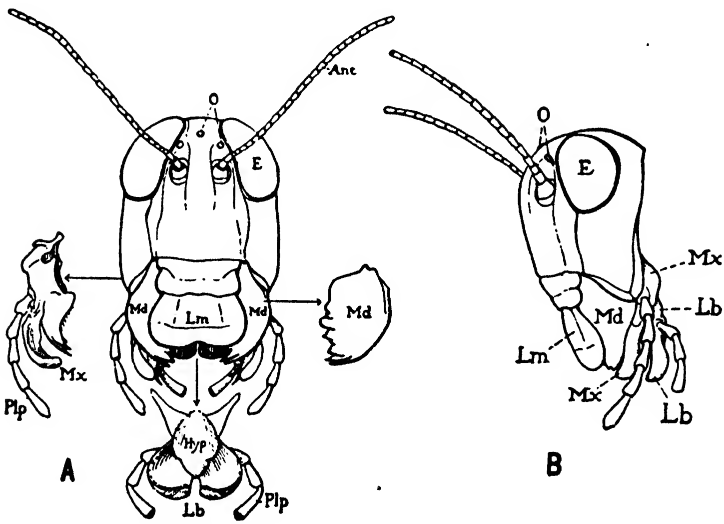

Fig. 60. Head of grasshopper, showing appendages and chief organs. *A,* anterior aspect; *B,* lateral aspect. *Ant,* antenna; *E,* compound eye; *Hyp,* hypopharynx; *Lb,* labium; *Lm,* labrum; *Md,* mandible; *Mx,* maxilla; *O,* ocelli; *Plp,* palpus. (After Snodgrass)

pharynx, bearing the opening of the salivary duct. On each side of this floor hang down the three pairs of appendages forming the chewing organs or mouthparts, consisting of the mandibles, maxillae, and labium. These articulate with the ventral margin of the capsule. The posterior portion of the head is shaped like an inverted horseshoe, the capsule forming the dorsal and lateral portion, the labium closing the bottom of the shoe; the open center is called the occipital foramen, through which pass the oesophagus, nerve cord, salivary duct, aorta, tracheae, and free blood. Inside the head is a series of braces called the tentorium, fig. 64.

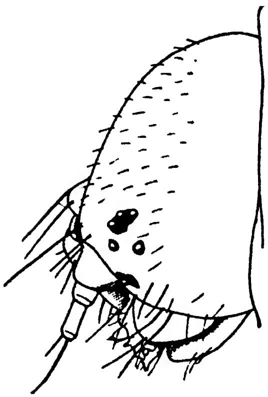

FIG. 61. Head of a caterpillar showing the ocularium. (From Folsom & Wardle, "Entomology," by permission of The Blakiston Co.)

Appendages of the Capsule. The eyes, ocelli, antennae, and labrum are considered to be fundamentally different from true segmental appendages, such as the mouthparts. They are thought to be homologues of the prostomial tentacles of the Annelida. These parts are nearly always present and are some of the most constant features of insect anatomy.

Compound eyes are usually large many-faceted structures situated on the dorsolateral portion of the capsule. Each eye is situated on or surrounded by a narrow ringlike or shelflike *ocular sclerite*. In many forms, especially larvae, the eyes are reduced to a single facet. In certain larvae they are represented by a group of separate facets, and the group is called an *ocularium*, fig. 61. In adult insects the number of facets may be extremely large. The housefly has about four thousand facets to an eye, and some beetles about twenty-five thousand.

Ocelli are three single-faceted organs situated on the face and usually between the compound eyes. The upper two are arranged as a pair, one on each side of the meson, and are called the lateral ocelli. The lower one is on the meson and is the median ocellus.

Antennae are a pair of movable segmented appendages which arise from the face, usually between the eyes. They articulate in the antennal socket, which is sometimes surrounded by a narrow ringlike antennal sclerite. The periphery of the socket has a small projection on which the antenna articulates. Antennae are extremely varied in shape, and names have been applied to the more striking types. A few examples are listed here and illustrated in fig. 62:

Filiform or threadlike.
Setaceous or tapering.
Moniliform or beadlike.
Serrate or sawlike.
Clavate or clubbed.
Capitate or having a head.
Lamellate or leaflike
Pectinate or comblike.

Labrum is the movable flap attached to the ventral edge of the face. The inner side of the labrum forms the front of the preoral cavity and is called the *epipharynx.* The epipharynx frequently bears

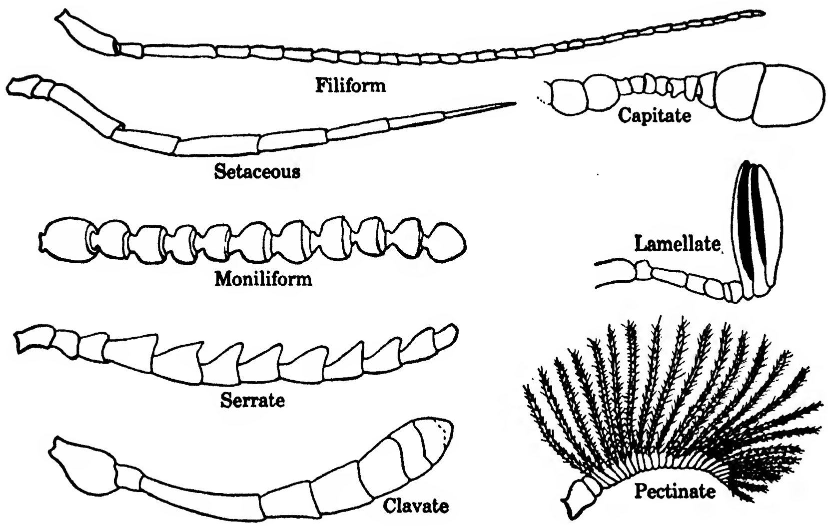

FIG. 62. Types of antennae.

raised lobes and complicated sets of sensory papillae and setae. These have proved very useful to the taxonomist as an aid in the identification of larval forms.

Principal sutures and areas. The head capsule is subdivided by several sutures. Most of these are considered to be secondary developments following the obliteration of the original segmental sutures. The principal head sutures and adjacent areas are as follows, fig. 63:

Vertex is the entire dorsum of the head between and back of the eyes.

Epicranial suture is a Y-shaped suture whose stem begins on the back of the head, crosses the vertex, and forks on the face. The stem is called the epicranial stem; the two arms of the forked portion are the epicranial arms.

Frons or front is the area on the anterior face which lies between or below the epicranial arms. The median ocellus occurs on this sclerite. It is bounded ventrally by the *frontoclypeal suture.*

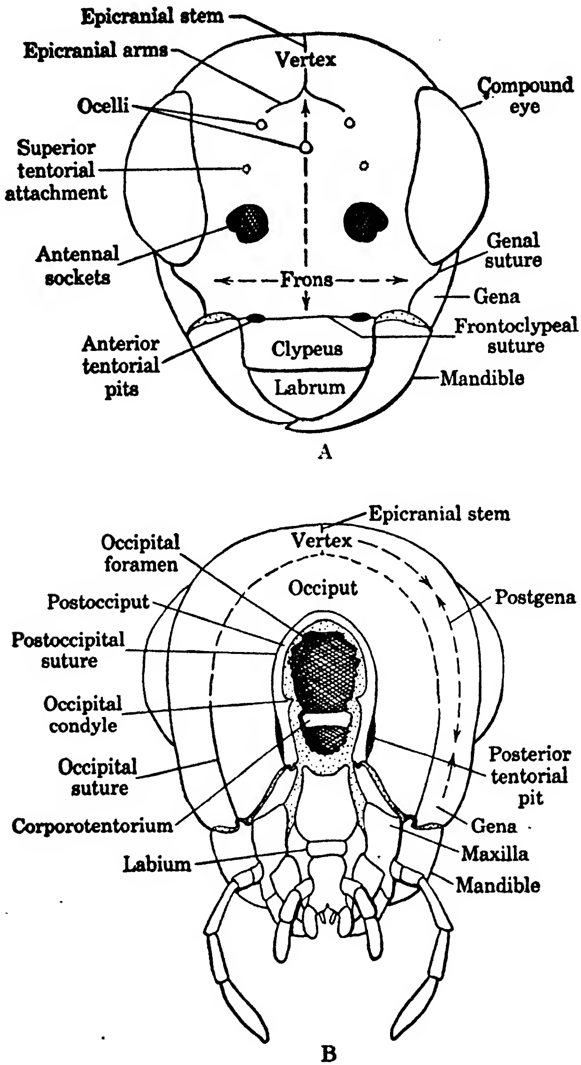

Fig. 63. Diagrams illustrating the principal sutures and areas of the head. *A*, anterior aspect (maxillae and labium omitted); *B*, posterior aspect.

Clypeus is the liplike area between the frontoclypeal suture and the labrum. It never articulates with the frons but is joined solidly with it. The *labrum* hangs below it and articulates by means of the membranous connection between them.

Gena is the lower part of the head beneath the eyes and posterior to the frons. There is sometimes a *genal suture* on the anterior

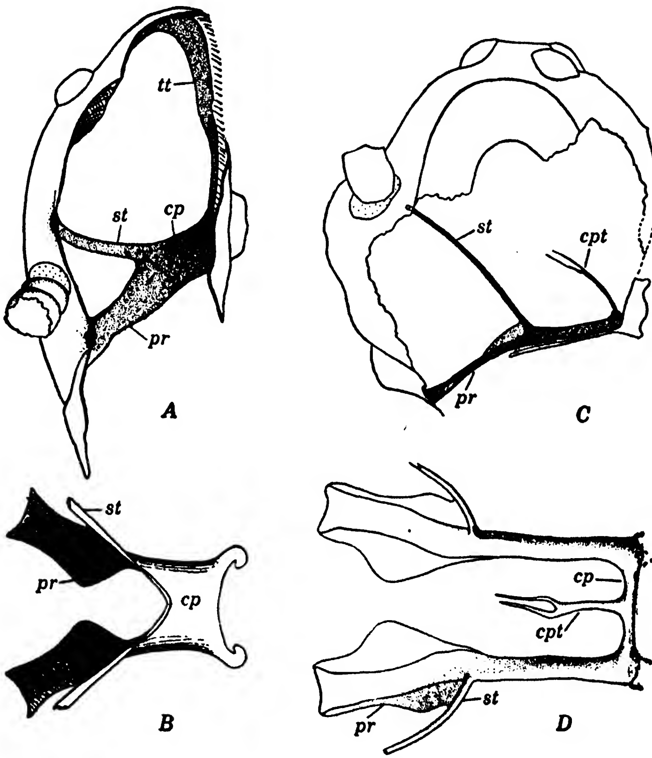

Fig. 64. Tentorium in Hymenoptera. *A*, head of *Macroxyela* cut away to show tentorium, lateral aspect; *B*, tentorium of same, dorsal aspect; *C*, head of *Aleiodes* cut away to show tentorium, lateral aspect; *D*, tentorium of same, dorsal aspect. *cp*, corporotentorium; *cpt*, corpotendon; *pr*, anterior arms; *st*, superior arms; *tt*, dorsal thickening extending from the tentorium along the side of the head.

portion of the face between the frons and gena; if this suture is absent, the division between frons and gena is indefinite. The area directly posterior to the eyes is called the postgena; there is no definite division between postgena and vertex or postgena and gena.

Occiput is the area comprising most of the back of the head. It is divided from the vertex and genae by the *occipital suture;* in many groups this suture is either reduced to a crease or completely obliterated in which case the occiput can be defined only as a general area merging anteriorly with vertex and gena.

Postocciput is the narrow ringlike sclerite which forms the margin of the occipital foramen. It is separated from the occiput by the *postoccipital suture,* almost universally present in adult insects. The postocciput bears the *occipital condyle* on which the head articulates with the cervical sclerites of the neck region.

Tentorium, Fig. 64. The head is strengthened internally by a set of sclerotized apodemes or invaginations of the body wall. These collectively form the tentorium, sometimes referred to as the endoskeleton of the head. In the apterygote or wingless groups of insects the parts of the tentorium are not always well developed. In most winged groups the tentorium is composed of four principal parts: the *anterior arms, posterior arms, corporotentorium* or central mass, and *dorsal arms.* The anterior arms are invaginated from the *anterior tentorial pits,* which usually are well defined externally as pits at each lower corner of the frons. The posterior arms are invaginated from the *posterior tentorial pits* which almost always persist as external slits on the postoccipital suture. The corporotentorium represents the inward extension, meeting, and fusing of the anterior and posterior arms. The dorsal arms are considered as secondary outgrowths of the anterior arms, because there is no large or persistent pit associated with their point of attachment with the head capsule, which is usually between the antennal sockets and lateral ocelli. The shape and relative position of the tentorial parts are extremely different in various groups of insects.

The Mouthparts

The three most conspicuous elements of insect mouthparts are the mandibles, maxillae, and labium. These represent modifications of typical paired arthropod limbs. The shape of these parts in insects is so different from that in the original ancestral forms that evidence from other arthropod groups is necessary to demonstrate the relationship. A study of the appendages of fossil arthropods, together with an analysis of the comparative morphology of appendages of living forms, indicates that all present-day arthropod appendages arose from a simple generalized form.

Generalized Arthropod Appendage, Fig. 65. The basal segment or *coxopodite* is implanted in the side of the body wall. The apical segments form the *telopodite*. Each segment has potentialities for developing processes on both the lateral and mesal sides, the lateral

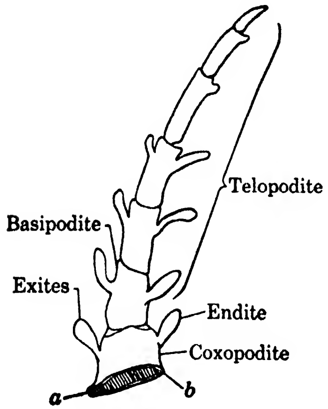

FIG. 65. Hypothetical arthropod appendage. (Modified from Snodgrass)

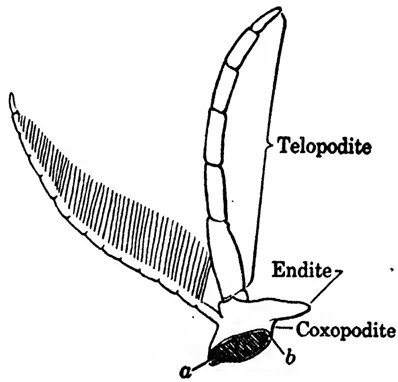

FIG. 66. Leg of a trilobite. (Redrawn from Snodgrass)

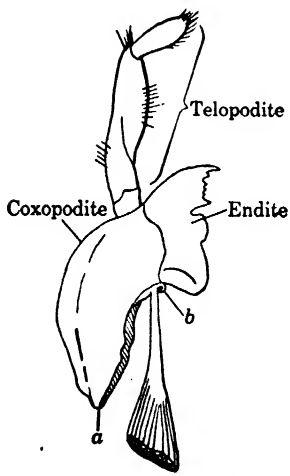

FIG. 67. Mandible of the crustacean *Anaspides*. (Redrawn from Snodgrass)

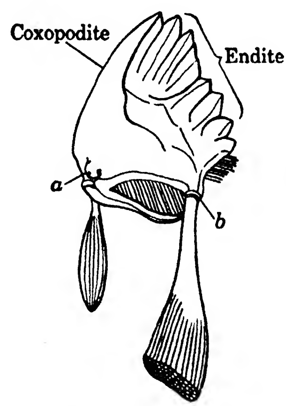

FIG. 68. Mandible of a grasshopper. (Redrawn from Snodgrass)

processes called *exites*, and the mesal processes called *endites*. A primitive and early modification is illustrated by the leg of the trilobite, fig. 66. Note that the coxopodite has a gill-like exite and a spur-like endite; the telopodite is simple and without processes.

Second Antennae, Chelicerae. These structures, belonging, respectively, to the Crustacea and the Arachnida, are appendages of the first postoral segment, fig. 13*B–D*. There is no definite evidence of appendages on the heads of living Insecta which represent them. Presumably, they were lost in an early evolutionary stage.

Mandibles, Figs. 60, 68. These are the anterior or first pair of true insect mouthparts and lie directly behind the labrum. They are appendages of the second postoral segment. Typically they are hard and sclerotized and have various sets of teeth and brushes. They articulate with the head at the base of the lateral margin and (except in a few primitive insects) at the base of the mesal margin also. Near each of these articulations arise strong tendons which project into the head and serve as attachments for the strong muscles which operate the mandibles.

No insect mandibles preserve other characters which would assist in explaining how they were derived from a simple segmental appendage. In many Crustacea, however, the mandibles are of a much more primitive type, fig. 67. The muscular development indicates that this is a simple derivative of a form such as the trilobite leg, fig. 66. The chief modifications include (1) an enlargement and strengthening of the coxopodite, (2) development of its endite into a rasping toothed area, (3) loss of the exite, and (4) reduction of the telopodite. In all insect mandibles, fig. 68, the telopodite has been lost completely. The insectan mandible is therefore only a much-modified coxopodite and its endite.

Maxillae, Fig. 69. These lie directly behind the mandibles and are the appendages of the third postoral segment. The musculature indicates that their evolution follows very closely that of the mandible but with these differences: (1) A mesal articulation has *not* been developed, (2) the telopodite is retained as a tactile organ or palpus, (3) the coxopodite is divided, and (4) the endite has developed into two distinct movable lobes.

In entomological literature, little reference is made to the terms coxopodite, telopodite, endite, etc., which refer to the fundamental divisions and processes of arthropod appendages. In this account they have been used until now to assist the student in correlating insect parts with those of other Arthropoda. From this point on, however, it is pertinent to make a change in terminology and employ those terms usually applied in entomological usage. These terms refer to parts which are for the most part differentiated only in insects, and the terms are therefore necessary for accurate identification of the part or area.

The generalized type of maxilla is a masticating structure which is divided into several well-marked parts, fig. 69, as follows:

Cardo, the triangular basal sclerite which is attached to the head capsule, and which serves as a hinge for the movement of the remainder of the maxilla.

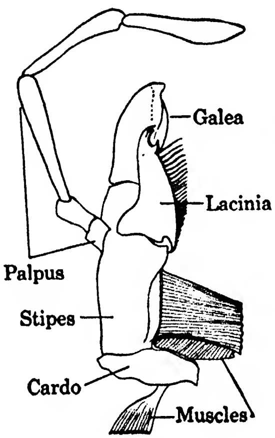

FIG. 69. Maxilla of a cockroach, illustrating a generalized type. (After (Snodgrass)

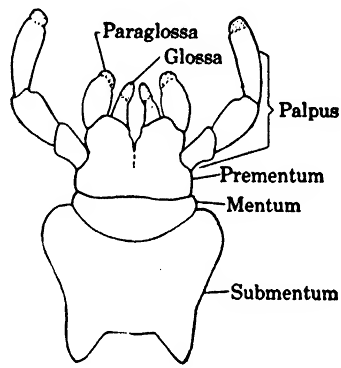

FIG. 70. Labium of a cockroach, illustrating a generalized type. (Adapted from Imms)

Stipes, the central portion or body of the maxilla, usually somewhat rectangular in shape. The stipes is situated above the cardo and is the basis for the remaining parts of the maxilla.

Galea, the outer (lateral) lobe articulating at the end of the stipes. It is frequently developed as a sensory pad or bears a cap of sense organs.

Lacinia, the inner (mesal) lobe articulating at the apex of the stipes. It is usually mandible-like in general form with a series of spines or teeth along its mesal edge.

Palpus, the antenna-like segmented appendage which arises from the lateral side of the stipes. It is commonly five-segmented. Presumably, it is entirely sensory in function.

Labium, Fig. 70. This structure forms the lip posterior to the maxillae. It appears to be a single unit but really consists of a second pair of maxillae which have fused on the meson to form a single functional structure. The parts of the labium correspond very closely to those of the maxillae, and their homologies have been established by studies of muscles and their point of attachment.

Postlabium, the basal region of the labium, which hinges with the head membranes. It is frequently divided into two parts: a basal

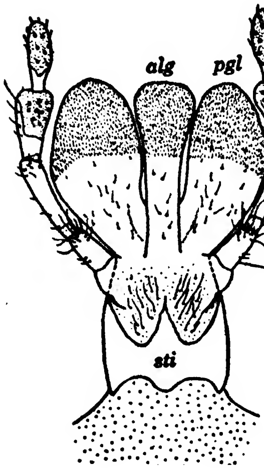

FIG. 71.

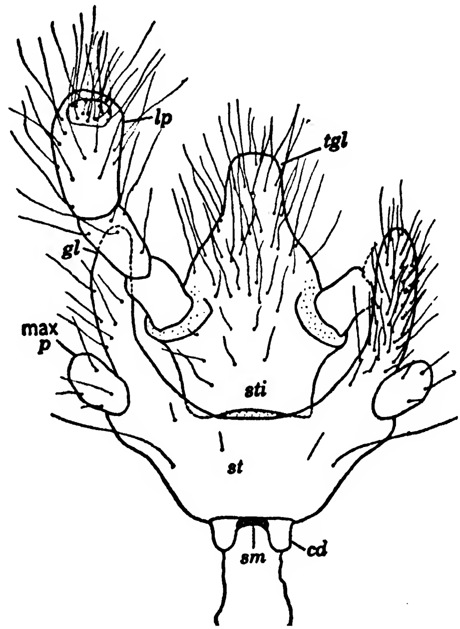

FIG. 72.

FIG. 71. Part of labium of hymenopteron *Trichiosoma triangulum,* illustrating an alaglossa. *alg,* alaglossa; *p,* palpus; *pgl,* paraglossa; *sti,* stipulae.

FIG. 72. Labium and fused maxillae of hymenopteron *Tremex columba,* illustrating a totoglossa. *cd,* cardo; *gl,* fused galea and lacinia; *lp,* labial palpus; *max p,* maxillary palpus; *sm,* submentum; *st,* fused stipites; *sti,* stipulae; *tgl,* totoglossa.

submentum and an apical *mentum.* The postlabium represents the fused cardo of the maxillae.

Prelabium, the apical region of the labium, including various lobes and processes. The central portion or body is the *prementum* (sometimes also called *stipulae*), which bears a pair of *labial palpi,* one on each side of the prementum, and each usually three-segmented in generalized forms.

The apical portion of the prelabium frequently forms a sort of tongue and for this reason is called the *ligula.* It varies greatly in structure but usually is divided into two pairs of lobes: (1) the *glossae,* a pair of mesal lobes usually close together, and (2) the *paraglossae,* a pair of lateral lobes which usually parallel the glossae. In many groups such as the Hymenoptera, the glossae are fused to form an *alaglossa,* fig. 71. In other cases the glossae and paraglossae may be fused together into a single solid lobe, which is called a *totoglossa,* fig. 72.

The following table illustrates the homologies of the corresponding parts of the maxillae and labium. When consulting this table refer also to figs. 69 and 70.

MAXILLA		LABIUM
cardo	corresponds to	postlabium { submentum, mentum }
stipes	corresponds to	prementum or stipulae
palpi	corresponds to	palpi
lacinia	corresponds to	glossae
galea	corresponds to	paraglossae

Hypopharynx. From the ventral membranous floor of the head arises the hypopharynx, fig. 73. It usually forms a protruding lobe

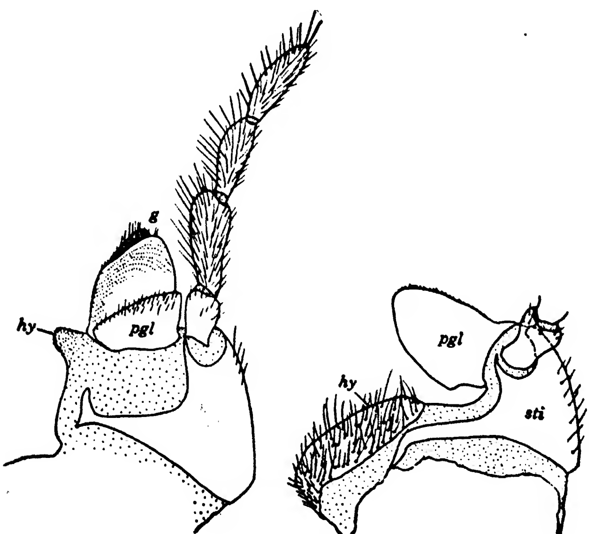

FIG. 73. Labium and hypopharynx of a sawfly *Arge pectoralis* (right), and a braconid *Aleiodes terminalis* (left). *g,* glossae; *hy,* hypopharynx; *pgl,* paraglossa; *sti,* stipulae.

or mound. In generalized insects the hypopharynx is so closely associated with the base of the labium as to be considered a part of it. Unlike the other mouthparts, the hypopharynx is not an appendage but an unsegmented outgrowth of the body wall.

Principal Types of Mouthparts

Insect mouthparts have become modified in various groups to perform the ingestion of different types of food and by different methods. The more diverse and interesting types are listed here, chosen to illustrate the varied shapes assumed by homologous parts, and the different uses to which they may be put. Many other types exist, many of them representing intermediate stages between some of the types treated here.

Chewing Type. In this type the various appendages are essentially as in the preceding figs. 68, 69, and 70. The mandibles cut off and grind solid food, and the maxillae and labium push it into the oesophagus. Grasshoppers and lepidopterous larvae are common examples. It seems certain that the chewing type of mouthparts is the generalized one from which the other types developed. This view is upheld by important evidence of two kinds. In the first place such mouthparts are most similar in structure to those of the centipedes and symphylids, which are the closest allies of the insects. In the second place, chewing mouthparts occur in almost all the generalized insect orders, such as the cockroaches, grasshoppers, and thysanurans; and they occur in the larvae of at least the primitive families of the holometabolous orders. In many of the holometabolous orders the adults frequently also have the chewing type of mouthparts which is little changed from the primitive type: for example, the Coleoptera and most of the Hymenoptera.

Cutting-Sponging Type, Fig. 74. In horseflies (Tabanidae) and certain other Diptera, the mandibles are produced into sharp blades, and the maxillae into long probing styles. The two cut and tear the epidermis of a mammal, causing blood to flow from the wound. This blood is collected by the spongelike development of the labium and conveyed to the end of the hypopharynx. The hypopharynx and epipharynx fit together to form a tube through which the blood is sucked into the oesophagus.

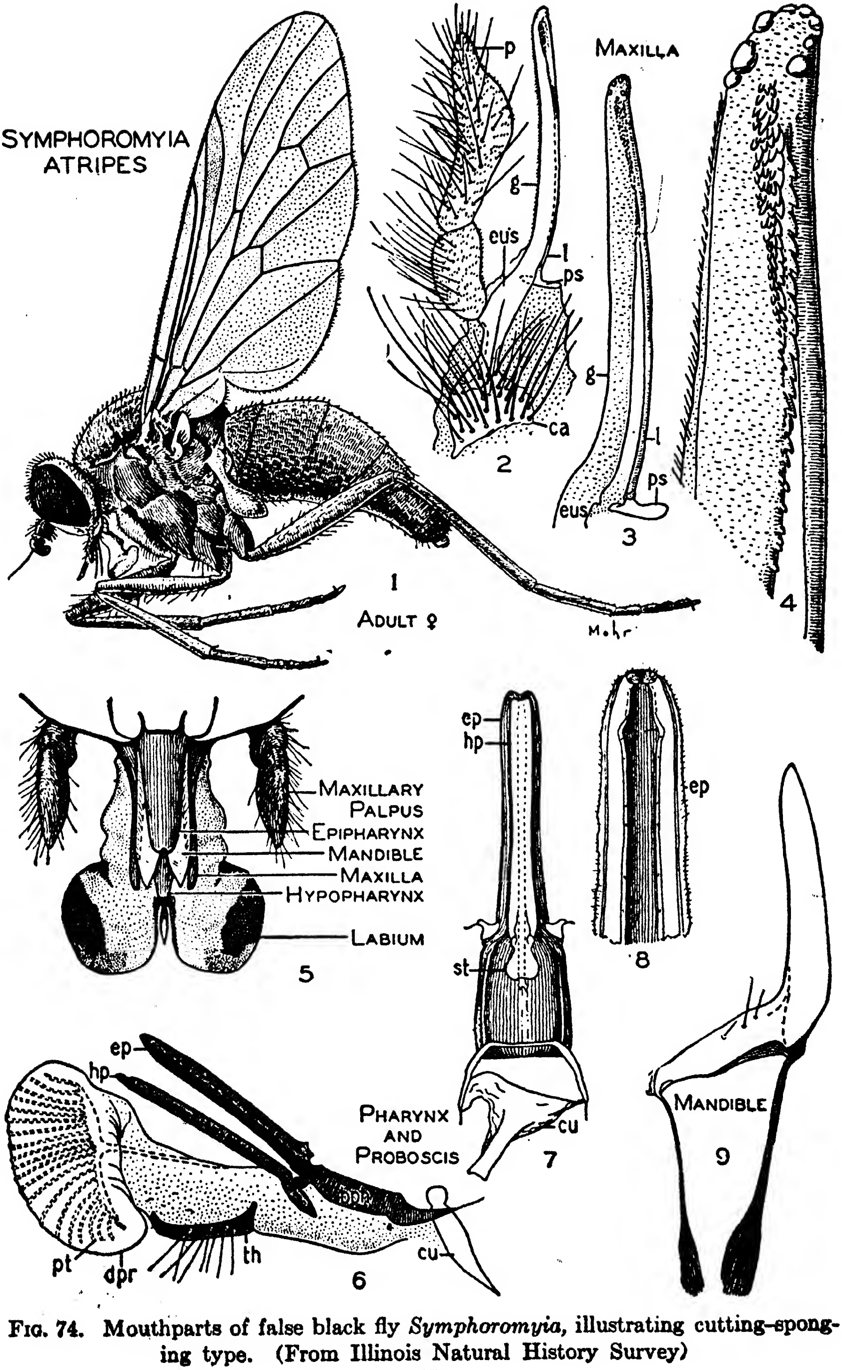

Fig. 74. Mouthparts of false black fly *Symphoromyia*, illustrating cutting-sponging type. (From Illinois Natural History Survey)

Sponging Type, Fig. 75. A large number of the non-biting flies, including the housefly, have this type, fitted for using only foods which are either liquid or readily soluble in saliva. This type is most similar to the cutting-sponging type, but the mandibles and maxillae are non-functional, and the remaining parts form a proboscis with a sponge-like apex, or labella. This is thrust into the liquid food, which is

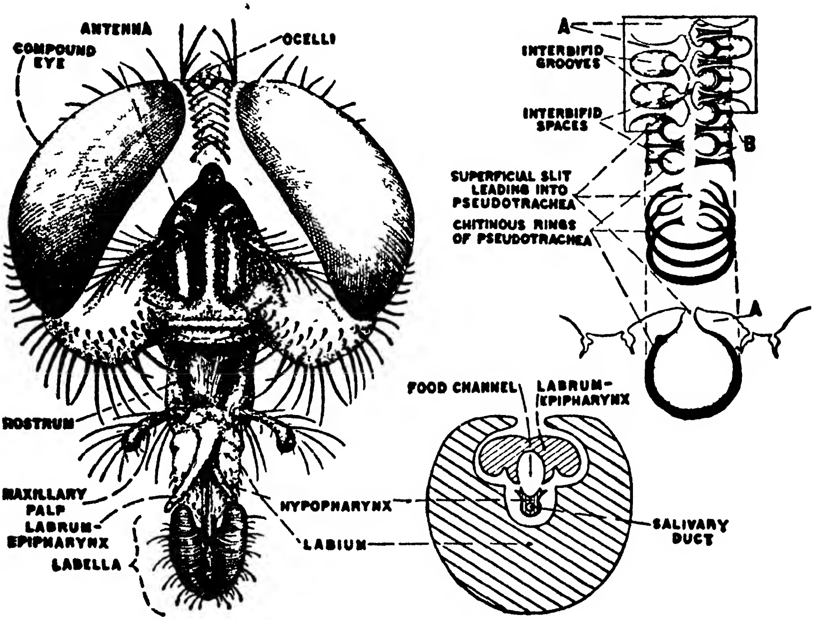

FIG. 75. Mouthparts of housefly, illustrating a sponging type. (From Metcalf and Flint, "Destructive and Useful Insects," by permission of McGraw-Hill Book Co)

conveyed to the food channel by minute capillary channels on the surface of the labella. The food channel is formed in this type also by the interlocking elongate hypopharynx and epipharynx, which form a tube leading to the oesophagus. Certain solid foods, such as sugar, are eaten by flies with these mouthparts. This is accomplished as follows: First, the fly extrudes a droplet of saliva onto the food, which dissolves in the saliva; this solution is then drawn up into the mouth as a liquid.

Chewing-Lapping Type. Another type of mouthparts for taking up liquid food is found in the bees and wasps, exemplified by the honeybee, fig. 76. The mandibles and labrum are of the chewing type and are used for grasping prey or molding wax or nest materials. The maxillae and labium are developed into a series of flattened elongate structures, of which the alaglossa (usually called the glossa) forms an extensile channeled organ. This latter is used to probe deep into nectaries of blossoms. The other flaps of the maxillae and labium fit up against the glossa and form a series of channels down which the

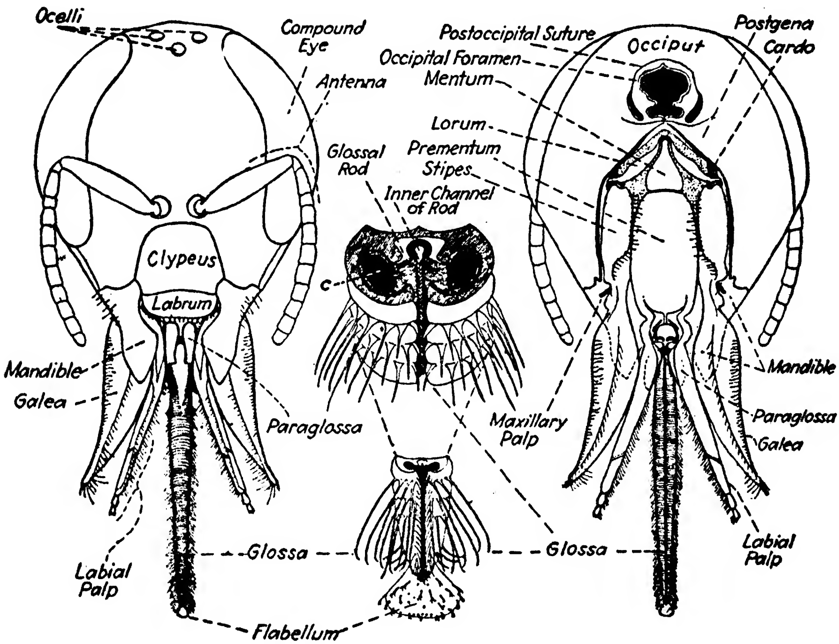

FIG. 76. Mouthparts of the honeybee, illustrating a chewing–lapping type. (From Metcalf and Flint, "Destructive and Useful Insects," by permission of McGraw-Hill Book Co.)

saliva is discharged and up which food is drawn. There is some difference of opinion among observers as to the exact mechanics by which passage of the liquids is attained.

Piercing–Sucking Type, Fig. 77. The mouthparts of many groups of insects are modified to pierce tissue and suck juices from them. This includes aphids, cicadas, leafhoppers, scale insects, and others which suck juices from plants; assassin bugs, water striders, and predaceous forms of many sorts which suck juices from insects and other small animals; and mosquitoes, bedbugs, lice, and fleas, which suck blood from mammals and birds. In this group the labrum, mandibles, and maxillae (sometimes the hypopharynx also) are slender and long and fit together to form a delicate hollow needle. The labium forms a

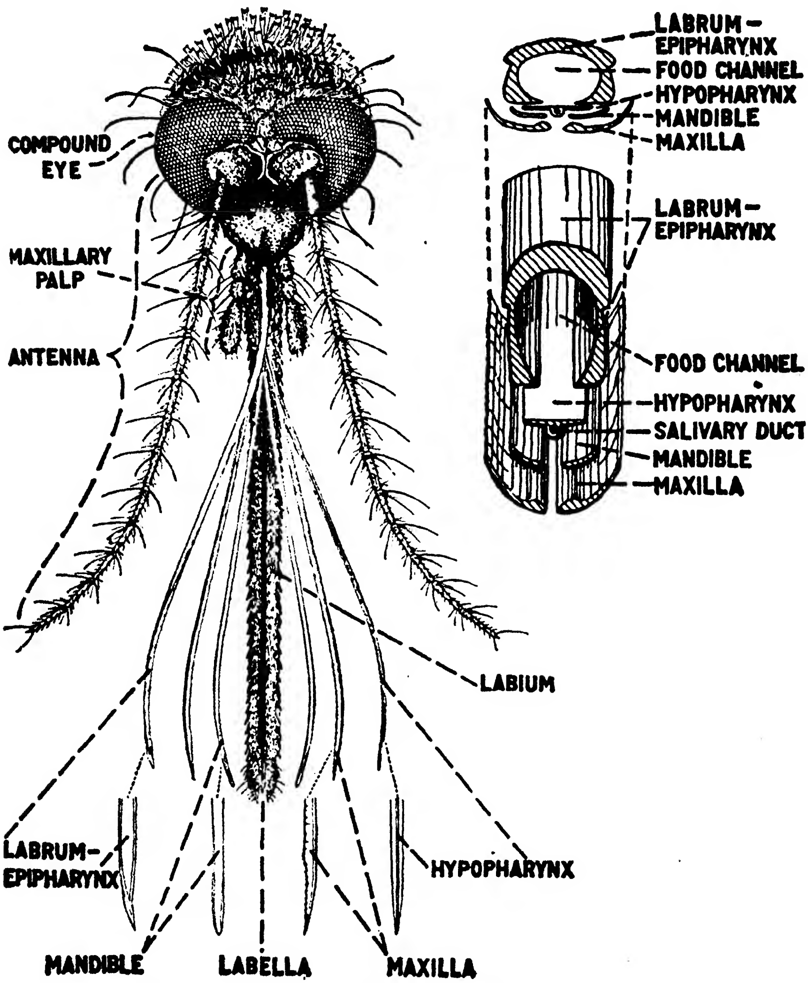

FIG. 77. Mouthparts of female mosquito, illustrating a piercing-sucking type. (From Metcalf and Flint, "Destructive and Useful Insects," by permission of McGraw-Hill Book Co.)

stout sheath which holds this needle rigid. The entire structure is called a beak. To feed, the insect presses the entire beak against the host, then inserts the needle into the host tissues, and sucks the host juices through the needle into the oesophagus.

An interesting and apparently generalized kind of this type of mouthparts is found in the thrips (see p. 271). Several components of the mouthparts are stylet-like but together form a rasping cone rather than a beak. On the extreme of complexity are the sucking lice or Anoplura, which have definite retractile beaks whose structure is so modified that the homologies of the parts are uncertain (see p. 273).

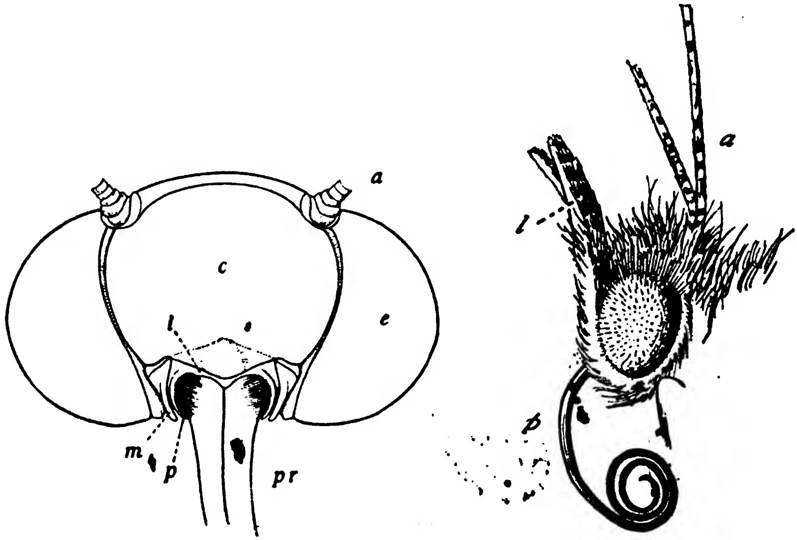

FIG. 78. Mouthparts of Lepidoptera, illustrating a siphoning type. Left, of a moth: *a*, antenna; *c*, clypeus; *e*, eye; *l*, labrum; *m*, mandible; *p*, pilifer; *pr*, proboscis. Right, of a butterfly: *a*, antennae; *l*, labial palpus; *p*, proboscis. (From Folsom and Wardle, "Entomology," by permission of The Blakiston Co.)

Siphoning-Tube Type, Fig. 78. Adult Lepidoptera feed on nectar and other liquid food. These are sucked up by means of a long proboscis, composed only of the united galea of each maxilla. These form a tube which opens into the oesophagus.

CERVIX OR NECK

Between the head and trunk is a membranous region which forms a neck, or *cervix*. This has sometimes been regarded as a separate body segment, the microthorax, but little evidence has been found to support this view. It seems more likely that the cervix includes areas of both the labial head segment and the prothoracic segment to form a flexible area between the two.

Imbedded in the cervix are two pairs of *cervical sclerites*, fig. 79, which serve as a point of articulation for the head with the trunk. The two sclerites on each side are hinged with each other to form a single unit, which articulates anteriorly with the occipital condyle on the postocciput of the head and posteriorly with the prothorax. Frequently the cervical sclerites are fused with the pleurae of the prothorax.

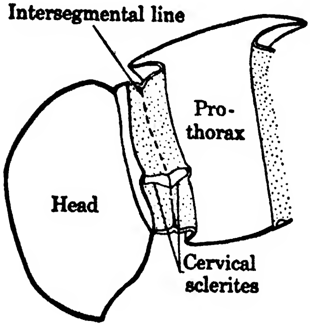

Fig. 79. Diagram of the cervical sclerites of an insect. (Modified from Snodgrass)

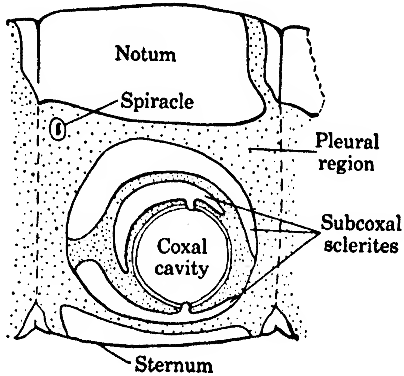

Fig. 80. Diagram of a simple insect body segment. (Redrawn from Snodgrass)

DEVELOPMENT OF THE GENERALIZED INSECT SEGMENT

The structure of existing Chilopoda and primitive insects suggests that the body segments of both groups evolved from a very simple type, fig. 80, composed of five elements:

1. The tergum or sclerotized dorsal plate, called the notum when referring to the thoracic tergum.
2. The sternum or sclerotized ventral plate.
3. The pleural region connecting tergum and sternum; it is entirely membranous.
4. A pair of segmented legs; the basal segment or coxopodite of each leg is embedded in the membrane between the tergum and sternum. The coxopodite is divided into a basal portion (*subcoxa*) and an apical portion (*coxa*). In fig. 80 the subcoxa is divided into three sclerites.
5. A pair of spiracles, one in the membrane above each leg.

In a few archaic groups of insects and in the Chilopoda is found a type of segment, fig. 81, which represents the simple prototype.

The tergum and sternum are unchanged. The subcoxa is represented by crescentic sclerites, or areas, one mesad of the coxa, and two laterad of it. The latter two appear to be units between the coxa of the leg and the tergum. These detached subcoxal sclerites in the pleural region are the forerunners of the pleural sclerites. The coxa forms the functional articulating base of the leg.

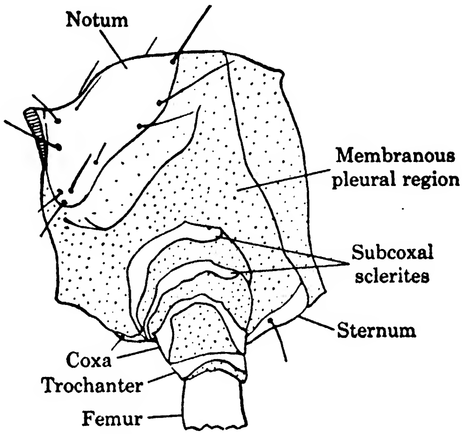

Fig. 81. Mesothorax of a proturan *Acerentomon*. (Redrawn from Snodgrass)

In the next evolutionary development, fig. 82, the subcoxal sclerites became immovably implanted in the segmental wall to form a solid base on which the functional leg articulates. The mesal subcoxal sclerites fused with the sternum, and the lateral subcoxal sclerites became flattened adjacent sidepieces together called the pleuron (pl., *pleura*). This condition is considered the generalized one from which developed both the specialized thoracic wing segments and the simplified abdominal segments. It is illustrated by many living forms, notably in the thorax of the immature stages of many such diverse groups as stoneflies, caddisflies, and lacewings, fig. 82.

THORAX

The thorax is the body region between the head and abdomen. It is composed of three segments, the prothorax, mesothorax, and metathorax, respectively.

In those orders which never developed wings, the three segments are nearly alike in general structure. The tergum and sternum are platelike, and the pleural sclerites (the subcoxal arcs) are small or degenerate, fig. 81.

In the orders of winged insects, the three thoracic segments are extremely dissimilar. The prothorax has essentially the same parts as the basic condition, fig. 82, although the various sclerites may be consolidated or recombined to such an extent that their exact interpretation may be difficult. The mesothorax and metathorax have undergone a veritable morphological revolution to accommodate the musculature necessary to combine both running and flying mechanisms

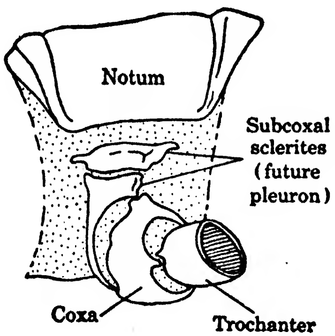

FIG. 82. Prothorax of a stonefly nymph. *Perla*. (Redrawn from Snodgrass)

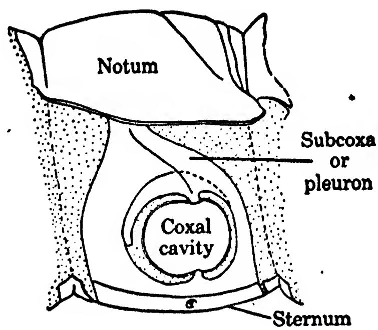

FIG. 83. Diagram of a hypothetical step in the development of a winged segment. (Redrawn from Snodgrass)

in one segment. Many new sclerites have been added, and many of them regrouped.

Generalized Winged Segment. There are three principal areas in this segment as in the general wingless one: the tergum (called the *notum* when applied to segments of the thorax), the sternum, and the pleura. The derivation of these from the primitive body segment is shown diagrammatically in fig. 83. Each has many specializations, but those of the pleura are the most conspicuous external features accompanying the winged condition. In existing forms of winged insects the parts follow the generalized condition illustrated in fig. 84.

Pleuron. This sclerite has become enlarged to form a conspicuous lateral plate. It has a ventral coxal process against which the leg articulates and a dorsal wing process against which the wing articulates. The pleuron is divided into an anterior portion, the *episternum*, and a posterior portion, the *epimeron*, by *a pleural suture* which extends from the coxal process to the wing process. This suture marks the line of invagination of the internal pleural apodeme, the *pleurodema.* Anteriorly and posteriorly the pleuron is fused with the sternum, the areas of fusion forming bridges before and behind the coxal cavities.

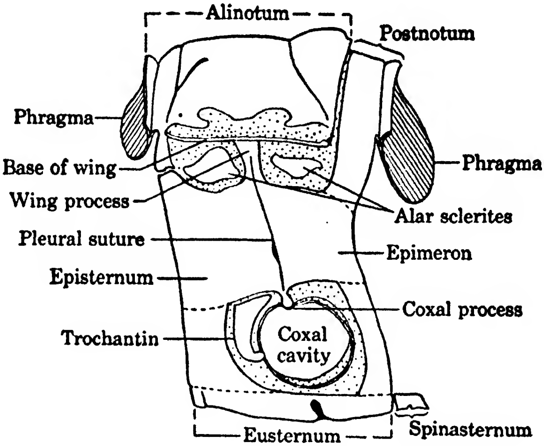

FIG. 84. Diagram of a typical winged segment. (Redrawn from Snodgrass)

Notum. This area is divided into two principal sclerites, the anterior *alinotum* and the posterior *postnotum.* The alinotum has an anterior apodeme or *phragma* and also is the sclerite connecting directly with the wing. It is subdivided in various patterns in different groups. The postnotum also bears a phragma and is connected laterally not with the wings but with the epimeron of the pleura to form a bridge behind the wings. The postnotum really is a part of the next posterior segment which has become a functional part of the one in front. Transpositions of this type are frequent in insects.

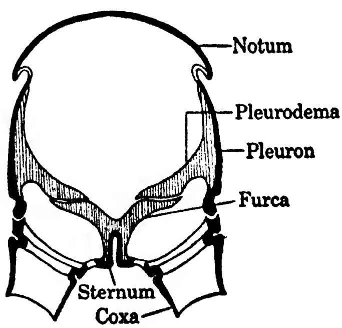

FIG. 85. Diagrammatic cross section of thoracic segments illustrating the furca and pleurodemae. (Redrawn from Snodgrass)

Sternum. This plate is joined by anterior and posterior bands to the pleura, thus forming the socket in which the coxa is situated. The central portion, called the *eusternum,* has a furrow which marks the line of invagination of the large internal apodeme called the *furca,* so named because it is forked or double at its apex, fig. 85. Posterior to the eusternum is a small sclerite, the *spinasternum,* bearing internally a single apodeme, the *spina.* This spinasternum had its origin in the membrane between the segments, but usually it is coalesced with the segment anterior to its place of origin.

Internal Skeleton. The various apodemes of the segments are frequently referred to collectively as the internal skeleton. They serve as areas of attachment for many of the large leg and wing muscles. The pleurodemae and furcae of a segment fit together closely as an almost continuous band, fig. 85.

Existing Forms. In a general discussion of the thorax it is impractical to go into more detail than the preceding outline because of the almost endless variety in the thoracic structure of existing insects. Many orders exhibit a distinctive basic pattern, and in large orders such as the Coleoptera and Diptera there may be many extreme modifications within the same order.

Often there is little apparent similarity between some existing form and the generalized type. In such cases identification of the sclerites must be preceded by orientation in relation to stabilized features or landmarks. The apodemes and the sutures which are their external indications, plus articulation points for legs and wings, are the most reliable.

Legs. The typical thoracic leg consists of six parts, the *coxa, trochanter, femur, tibia, tarsus,* and *pretarsus,* fig. 86*A*. The coxa is the segment which articulates with the body; it may bear a posterior lobe called the *meron.* The tarsus of adult insects is usually subdivided into two to five segments. The pretarsus appears as a definite small end segment of the leg in the Collembola but in all other insects is represented only by a complex set of claws and minute sclerites set in the end of the tarsus. The Collembola are also unique in that usually the tibia and tarsus are combined to form a single tibiotarsus.

In general, insects have simple legs designed for walking or running, fig. 86*A*. There have developed, however, a large number of modifications which fit the legs for other uses. These include jumping types with greatly enlarged femora, as in the grasshoppers, fig. 86*B;* grasping types armed with sharp opposing spurs and spines, fig. 86*C,* as in the praying mantis; swimming types, having long brushes of hair and flattened parts, as in the water boatmen; and digging types, with strong, scraper-like parts, fig. 86*E,* such as found in the mole crickets.

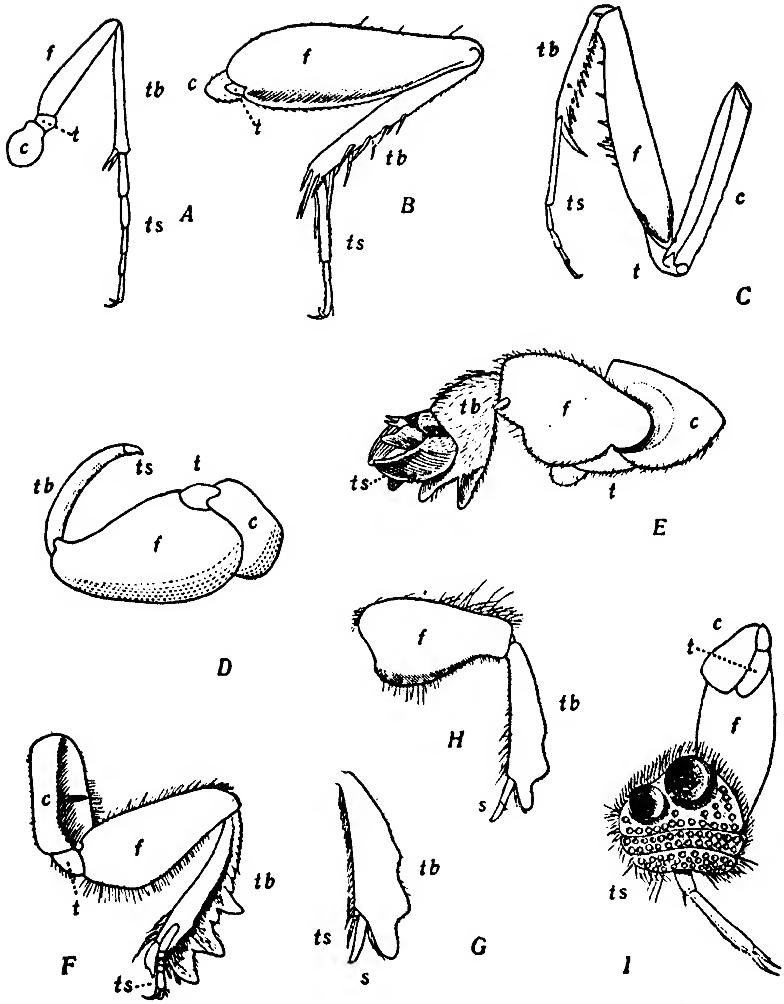

FIG. 86. Legs of insects adapted for: *A*, walking; *B*, jumping (hind leg of cricket); *C*, grasping (front leg of mantis); *D*, clasping (front leg of bug); *E*, digging (front leg of mole cricket); *F–H*, digging (front legs of beetles); *I*, holding fast by suction (front leg of male diving beetle). *c*, coxa; *f*, femur; *s*, spur; *t*, trochanter; *tb*, tibia; *ts*, tarsus. (From Folsom and Wardle, "Entomology," by permission of The Blakiston Co.)

Wings

The wings of insects are a type unique among all animals. In such flying animals as bats and birds, the wings are highly modified front legs. In insects this is not the case. Their wings are outgrowths of the body wall along the lateral margins of the dorsal plate or notum. Unlike most other insect appendages, the wings have no muscles attached inside them.

Wings, giving the power of flight, have been one of the most important reasons for the success of the insect group as a whole. No other invertebrate group has ever developed wings. Because flight is so characteristic of the insect group, it is treated here in more detail than other activities such as walking which are achieved by many animal groups.

Typically, pterygote insects have two pairs of wings, the mesothorax and metathorax each bearing a pair. The prothorax is always wingless. A few fossil forms are known in which the prothorax has lateral flaps, but there is no evidence to indicate that functional wings were ever developed on this segment.

Origin. The manner in which wings and flight were developed by insects is not certain. Known fossils of the most ancient winged insects had wings which were as well developed as those of present-day dragonflies. No intermediate types have been discovered between these groups with functional wings and the primitive wingless forms such as the silverfish.

The most widely accepted theory regarding their origin is that wings began as flat lateral extensions of the notum, which aided the insect in planing from a higher level to a lower one. A supposed early "planing wing" is shown in fig. 87. Such planing extensions presumably developed their first movement for deflection or warping to aid in steering. To accomplish flight, it was necessary for a hinge or flexible connecting link to develop between the wing and the body. In some insects, such as the dragonflies, flight development stopped at essentially this point. In most other insects, however, a mechanism developed for folding the wings back over the body when not in use.

Structure. In basic design, insect wings are very simple. They are a flaplike extension of the body wall, with an upper and lower membrane, between which run supporting "fibers" called veins. The base of the wing connects with the body by a membranous hinge in which are set a group of small sclerites called *axillary sclerites,* fig. 88.

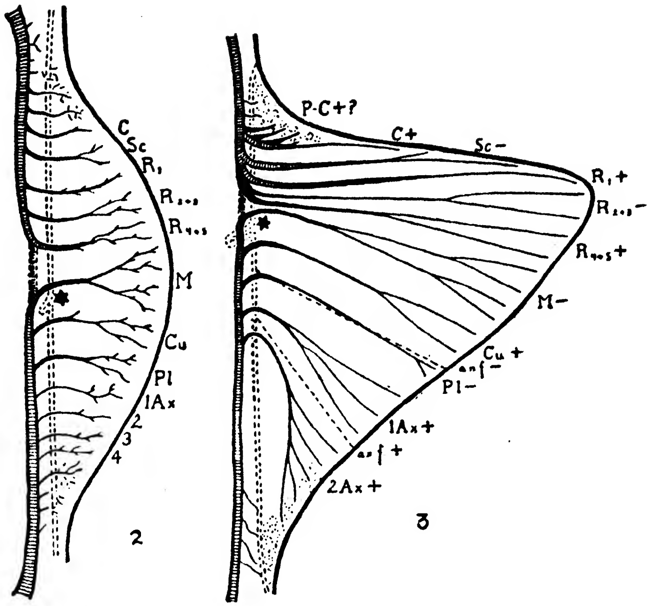

FIG. 87. Hypothetical planing wing of an insect. The venational interpretation is slightly different from that adopted in this book. (After Forbes, courtesy of "American Midland Naturalist")

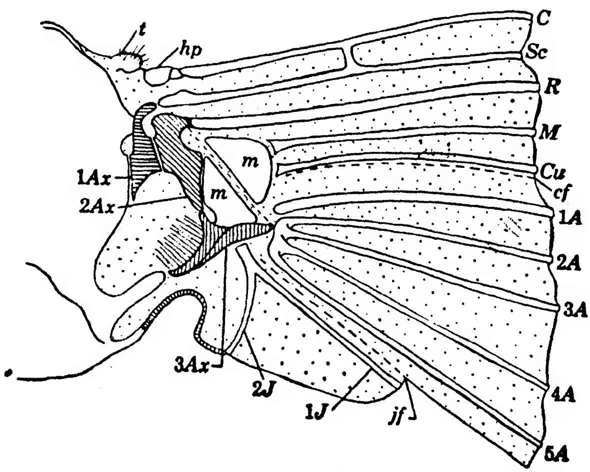

FIG. 88. Base of wing showing axillary sclerites connecting wing and thorax. *Ax*, principal axillary; *hp*, humeral plate; *m*, median plate; *t*, tegula. (Modified from Snodgrass)

These articulate with the edge of the notum. Closely associated with them are two small sclerites, the *basalar* and *subalar sclerites,* which lie one on each side of the wing process of the pleuron.

Venation. In most wings, fig. 89, there are many thickened lines which strengthen the thin membrane. Some of these lines run from the base of the wing toward the apex; these are called *veins.* Others run more or less crosswise of the wing and connect veins; these are

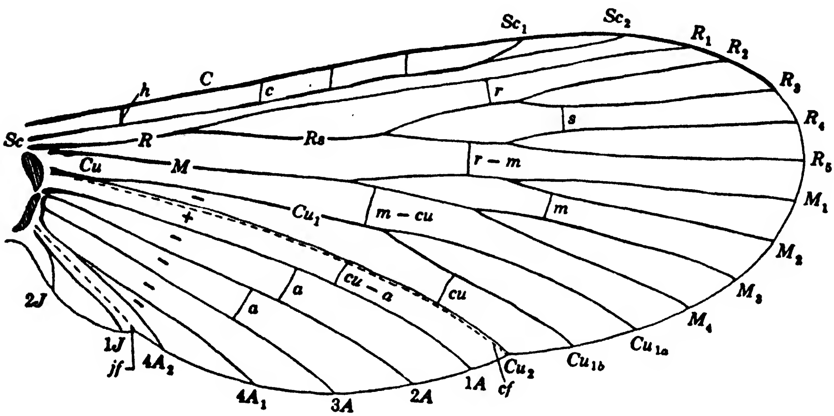

FIG. 89. Diagram of an insect wing showing typical veins and crossveins of modern insects.

called *crossveins.* The pattern of veins and crossveins is termed *venation.*

It seems certain that originally veins and crossveins developed from tracheae or air tubes running from the body into the wing and aerating the wing during its growth. These tracheae hardened, became detached at the base, and served as supports when the wing was fully formed.

The wings of insects exhibit innumerable differences in venation. These differences are of great importance in classification, because characters of venation identify many orders, families, and genera. All types of venation seem to have developed from the same basic pattern. This applies only to the main trunks of the veins.

A wing which illustrates the basic pattern of the veins is shown in fig. 89. This is diagrammatic, since no such exact wing is known, but it combines evidence gleaned from the conditions of many. Each main vein has been given a definite name; these are listed here in order of occurrence from the anterior to the posterior margin of the wing. Certain veins have definite typical branches. Standard abbreviations are indicated for the veins.

Costa (C) usually forms the thickened anterior margin of the wing. It is unbranched.

Subcosta (Sc) runs immediately below costa, always in the bottom of a trough between costa and radius. Typically subcosta is divided into two branches.

Radius (R) is the next main vein. It is a stout one and connects at the base with an axillary sclerite. It is divided into two main branches, R_1 and radial sector R_s. Radial sector is frequently divided into four main branches.

Media (M) is one of three veins articulating with some of the small median axillary sclerites. The base is usually in a depression. Typically it is divided into four branches, M_1, M_2, M_3, and M_4.

Cubitus (Cu) also articulates with the median axillary sclerites, and has two main branches. Its basal portion and Cu_2 are in a depression; but Cu_1 runs along a ridge and is usually branched.

Cubital furrow (cf) is a definite crease along which the wing folds. It is not a vein but is one of the most important landmarks for identifying the cubital and anal veins, which it separates.

Anal veins ($1A$, $2A$, $3A$, etc.) form a set which are united or close together at the base and closely associated with the third axillary sclerites, $3Ax$.

Jugal furrow (jf) is a crease separating the anal region or fold from the jugal fold, which is the small area at the basal posterior corner of the wing. This fold also is of the most stable wing landmarks.

Jugal veins ($1J$, $2J$) are short veins in the jugal fold.

Crossveins. Definite names are given to the kinds of crossveins, based on the veins which they connect. These crossveins have standard abbreviations which are never written in capital letters; these are outlined in Table 4. Numbers are used to denote individual cross-

TABLE 4. TERMINOLOGY OF CROSSVEINS

Veins Connected	*Name of Crossveins*	*Abbreviation*
Costa to subcosta or R_1	**Costal**	***c***
Branches of radius	**Radial**	***r***
Radius to media	**Radio-medial**	***r-m***
Branches of media	**Medial**	***m***
Media to cubitus	**Medio-cubital**	***m-cu***
Branches of cubitus	**Cubital**	***cu***
Cubitus to anal	**Cubito-anal**	***cu-a***
Various anals	**Anal**	***a***

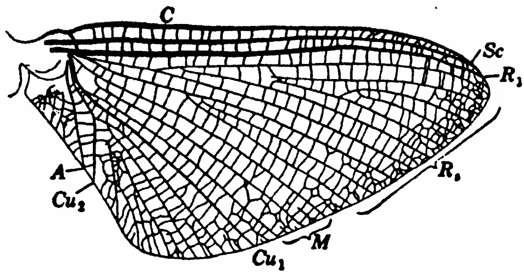

Fig. 90. Front wing of a mayfly.

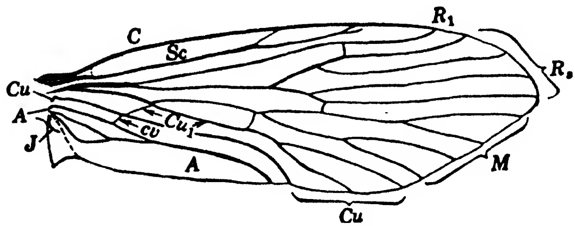

Fig. 91. Front wing of a caddisfly.

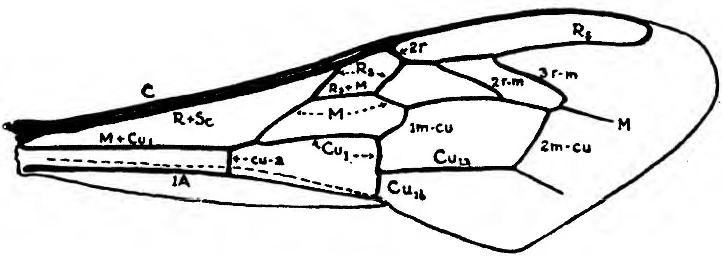

Fig. 92. Front wing of a honeybee.

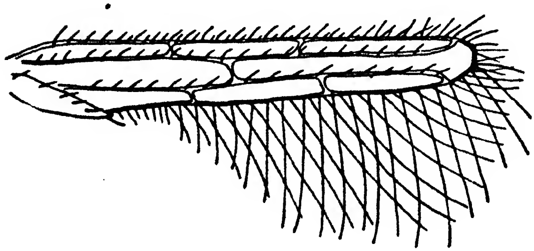

Fig. 93. Front wing of a thrips. (After D. L. Crawford)

veins in a series, for example, fourth costal crossvein, third radio-medial crossvein, and so on. There is one notable exception: The crossvein between costa and subcosta at the base of the wing is called the humeral crossvein and indicated by *h*. In orders such as the Trichoptera and Lepidoptera in which the crossveins are greatly reduced, the crossvein between R_1 and R_2 is called the radial *r*, and that between R_3 and R_4 is called the sectorial crossvein *s*.

Venational Evolution. In a primitive type of wing such as that of a mayfly, fig. 90, the veins branch profusely toward the margin, and the crossveins are extremely numerous. It is only near the base of the wing that the typical veins are apparent. There has been a steady evolution in almost every order of insects, however, toward a stronger supporting system for the wing. This has involved a reduction in the number of both crossveins and vein branches, usually accompanied by either a union of various main veins or a realignment of veins or both. The caddisfly wing, fig. 91, illustrates reduction of crossveins and marginal branches. In the honeybee wing, fig. 92, reduction of crossveins has not gone so far, but the veins have become reduced in

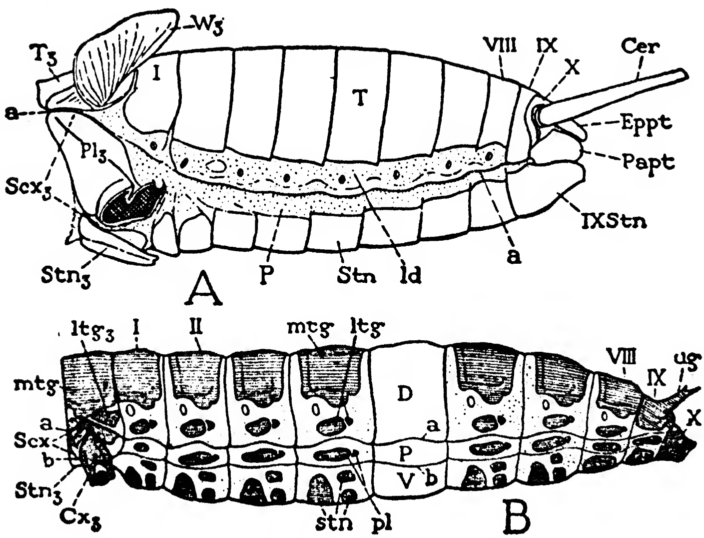

Fig. 94. Metathorax and abdomen of insects. *A*, adult cricket *Gryllus; B*, larva of ground beetle *Calosoma*. *a*, dorsopleural line; *b*, pleuroventral line; *Cer*, cercus; *Cx*, coxa; *D*, dorsal region; *Eppt*, epiproct; *ld*, laterodorsal membranous region; *ltg*, lateral pieces of tergite; *mtg*, mesal part of tergite; *P*, pleural region; *Papt*, paraproct; *pl*, pleura; *Scx*, subcoxal region; *Stn*, sternum; *T*, tergite; *Ug*, urogomphi; *V*, ventral region; *W*, wing. (After Snodgrass)

number, fused, and realigned. In the thrips wing, fig. 93, the venation *is so reduced that identification of the few remaining veins is almost impossible.*

ABDOMEN

The abdomen is the third and posterior region of the insect body. It is relatively simple in structure, compared with the thorax, and in adults has no walking legs. Primitively it is 12-segmented but this condition is distinct only in Protura, fig. 189, and certain embryonic stages. Usually the abdomen consists of 10 or 11 segments, fig. 94*A*. In some forms much greater reduction occurs, as in the Collembola which have only six abdominal segments, fig. 191. Many groups, such as the housefly group, have the last several segments developed into a copulatory structure or an ovipositor which is normally retracted within the preceding segments.

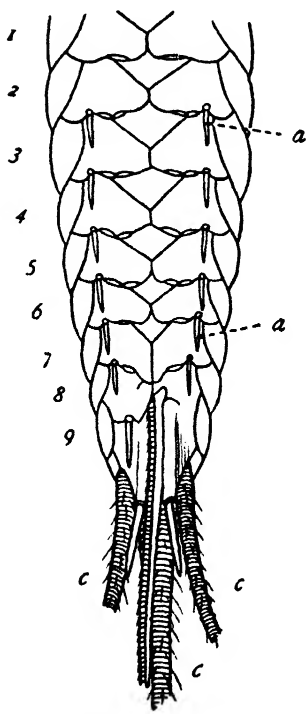

Fig. 95. Ventral aspect of the abdomen of a female *Machilis maritima*, to show rudimentary limbs (*a*) of segments 2 to 9. (The left appendage of the eighth segment is omitted.) *c, c, c,* lateral cerci and median pseudocercus. (From Folsom and Wardle after Oudemans)

Segmental Structure. In adult insects, a typical segment consists of (1) a tergum or dorsal plate, (2) a sternum or ventral plate, (3) lateral areas of membrane connecting tergum and sternum, and (4) a spiracle on each side, usually situated in the lateral membrane. In some larval forms, fig. 94*B*, and a few adults, there are sclerites in the lateral membrane; some of these undoubtedly represent vestiges of the subcoxal sclerites of the primitive appendages (see fig. 81, p. 81).

Appendages. These may be divided roughly into two groups: those not associated with reproduction, and those developed for reproductive activities such as mating or oviposition.

Non-reproductive Types. In most adult insects abdominal appendages are absent except on the terminal segments. A few primitive forms have retained degenerate legs represented by styli, as in the silverfish, fig. 95. The appendages of the eleventh segment, the cerci, are present in most insects, fig. 94*A*, *Cer.* They are usually

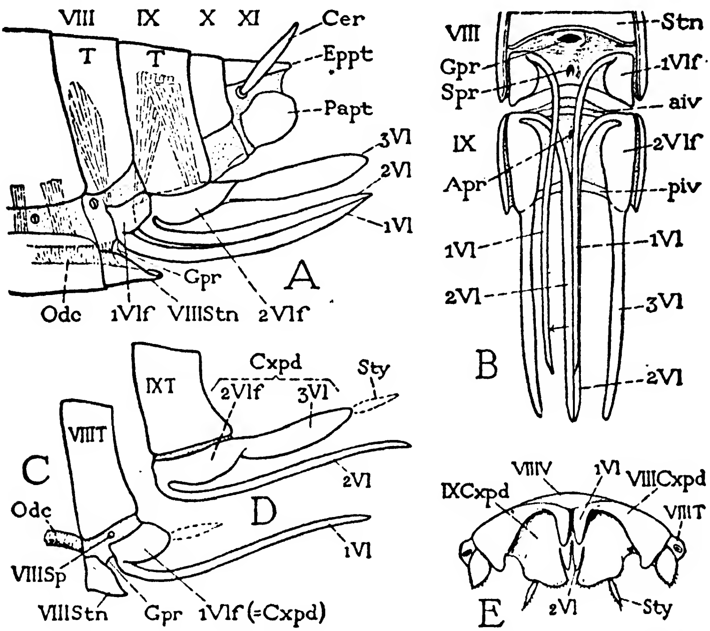

FIG. 96. Structure of the ovipositor of pterygote insects (*A–D*, diagrammatic). *A*, showing segmental relations of the parts of the ovipositor. *C*, *D*, lateral view of genital segments and parts of ovipositor dissociated. *E*, nymph of *Blatta orientalis*, ventral view of genital segments with lobes of ovipositor. *aiv*, anterior intervalvar space; *Apr*, aperture of accessory glands; *Cer*, cercus; *Cxpd*, coxopodite; *Gpr*, gonopore; *Odc*, oviduct; *piv*, posterior intervalvar space; *sp*, spiracle; *Stn*, sternite; *Sty*, stylus; *T*, tergite; *Vl*, valvula; *Vlf*, valvifer. (After Snodgrass)

tactile organs and in such groups as caddisflies become part of the male genitalia. The cerci may appear to belong to the tenth or ninth segment if the eleventh or tenth segment is reduced. In larvae and nymphs a great variety of abdominal appendages are developed. Well-known examples are the larvapods of caterpillars, fig. 58, and the segmental gills of mayfly nymphs, fig. 194.

Reproductive Types. These generally include appendages of the eighth and ninth segments in the female, but only of the ninth in the male.

Female. The typical ovipositor, fig. 96, is composed of three blades, the first, second, and third valvulae, respectively. The *first valvulae* 1*Vl* arise from a pair of plates, the *first valvifers* 1*Vf* of the eighth segment. The valvifer and valvula probably correspond to

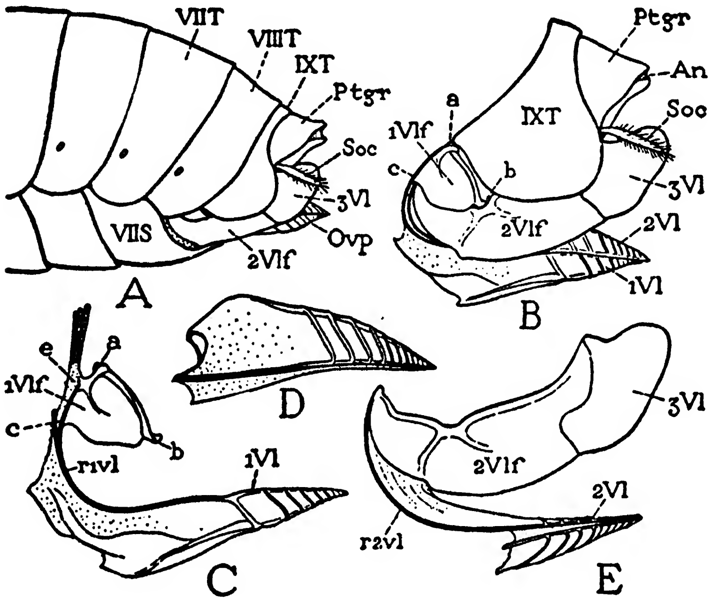

FIG. 97. The ovipositor of a sawfly. *A*, end of abdomen. *B*, showing relation of basal parts of ovipositor to each other and to ninth tergum. *C*, first valvifer and valvula. *D*, second valvula. *E*, second valvifer with second and third valvulae. In taxonomic papers on sawflies the first and second valvulae are termed the lancet and lance, respectively. *a, b, c, e,* articulation points of valvifer; *An*, anus; *Ovp*, ovipositor; *Ptgr*, pygidial or end segment; *r*, ramus; *Soc*, cercuslike appendage, often called socii; *T*, tergite; *Vl*, valvula; *Vlf*, valvifer. (After Snodgrass)

the coxopodite and telopodite of the generalized arthropod segment, fig. 65. The *second valvifers* 2*Vf* bear a ventral pair of blades, the *second valvulae* 2*Vl*, and a dorsal pair, the *third valvulae* 3*Vl*. In most insects with a well-developed ovipositor, such as the sawflies, fig. 97, the first and second valvulae form a cutting or piercing organ with an inner channel down which the eggs pass. The third valvulae form a scabbard or sheath into which the ovipositor folds when retracted. In Orthoptera, either all three pairs fit together to form the functional ovipositor, or the second valvulae form a short egg guide.

In many insects the valvulae are only poorly or not at all developed, in which case the apical segments of the abdomen generally form an extensile tube that functions as an ovipositor. This is exemplified by many of the Lepidoptera and Diptera, fig. 98.

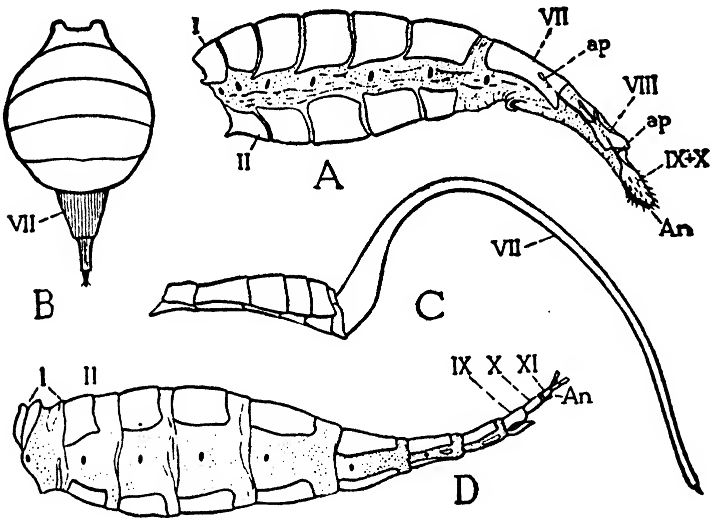

FIG. 98. Examples of an "ovipositor" formed of the terminal segments of the abdomen. *A*, a moth *Lymantria monacha* (from Eidmann, 1929). *B*, a fruit fly *Paracantha culta*. *C*, a fruit fly *Toxotrypania curvicauda*. *D*, a scorpionfly *Panorpa consuetudinis*. *ap*, apodeme; *An*, anus. (After Snodgrass)

Male. In this sex the appendages of the ninth segment are usually combined with parts of the ninth segment proper and sometimes parts of the tenth to form a copulatory organ. In each order this organ usually displays fundamental peculiarities. It is extremely difficult to homologize the individual parts of these copulatory organs throughout the insect orders or to be certain of their relation to what must have been the simple parts and appendages from which they are derived.

Structural differences in the copulatory organs furnish excellent taxonomic characters in many groups of insects for the differentiation of families, genera, or species. In any one group the constituent parts of the organ are usually well marked, and in each group there is a clear terminology for the designation of these parts. Until closer agreement is reached regarding the homologies of these structures in different orders, it is more practical to employ the terminology in established usage for any particular group. A simple type is illustrated by Thysanura, fig. 99, and a more complicated type occurs in

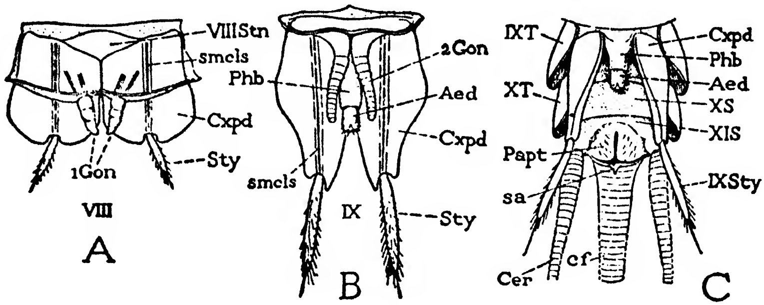

FIG. 99. Male genitalia of Thysanura. *A, Machilis variabilis,* dorsal view of first gonopods, showing gonapophyses of eighth segment. *B,* same, dorsal view of second gonopods and median copulatory organ. *C, Nesomachilis maoricus,* ninth and terminal segments, ventral view. *Aed,* aedeagus; *Cer,* cercus; *cf,* caudal filament; *Cxpd,* coxopodite; *Gon,* gonapophysis; *Papt,* paraproct; *Phb,* base of phallic or intromittent organ; *S,* sternite; *sa,* supra-anal plate; *smcls,* muscles of stylus, *Sty,* stylus; *T,* tergite. (After Snodgrass)

the caddisflies, fig. 100. These two examples by no means give the full range of different types among the insect orders but will serve to indicate some of the variety in structure which may be found.

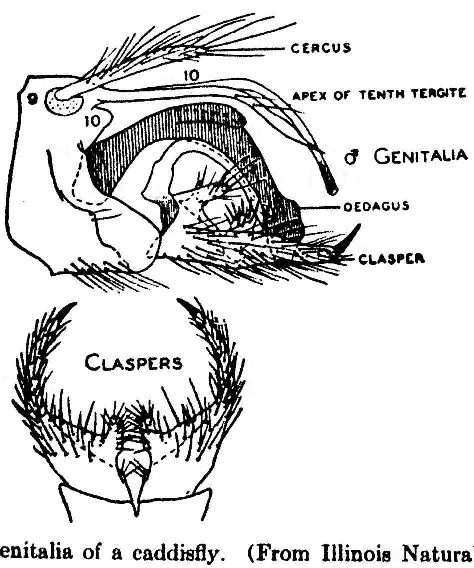

FIG. 100. Male genitalia of a caddisfly. (From Illinois Natural History Survey).

MUSICAL ORGANS

Insects make noises in various ways. In some cases the noise is produced by the insect's normal activities without aid of special noise-making structure. The most familiar example is the hum made by

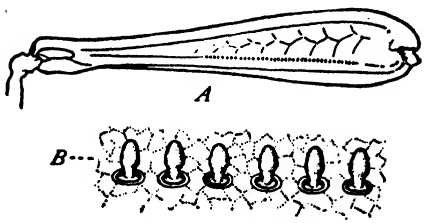

FIG. 101. File on inner face of hind femur of a cricket. *A*, hind femora of *Stenobothrus; B*, file greatly enlarged. (After Comstock, "An Introduction to Entomology," by permission of The Comstock Publishing Co.)

flying or hovering insects; the hum or note is produced by the extremely rapid vibrations of the wings.

A few insect groups have special sound-producing structures. The sound waves are produced by the vibration of a wing membrane, a

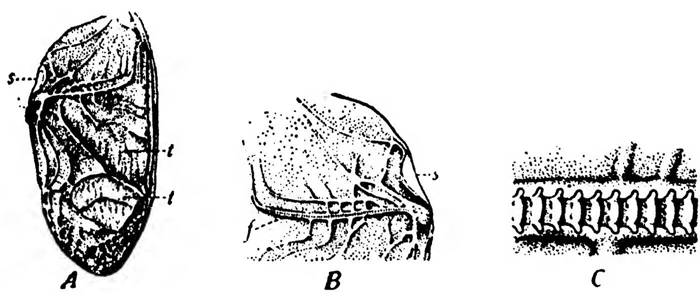

FIG. 102. Fore wing of *Gryllus*, showing file and scraper. *A*, as seen from above, that part of the wing which is bent down on the side of the abdomen is not shown; *s*, scraper; *t*, *t*, tympana. *B*, base of wing seen from below; *s*, scraper; *f*, file. *C*, file greatly enlarged. (After Comstock, "An Introduction to Entomology," by permission of The Comstock Publishing Co.)

specialized portion of the body wall, or special membranes. Those areas are set in motion by structures specialized for the purpose. Grasshoppers which produce a crackling sound have a simple mechanism. The front margin of the hind wing scrapes over the thickened veins of the fore wing, causing the latter to vibrate. In other grasshoppers the inner face of the hind femur is provided with a file of minute teeth, fig. 101; this file is rubbed over the fore wing to make the latter vibrate. Various crickets have a file on one or both wings, application of which causes a special area of the wing to vibrate, fig.

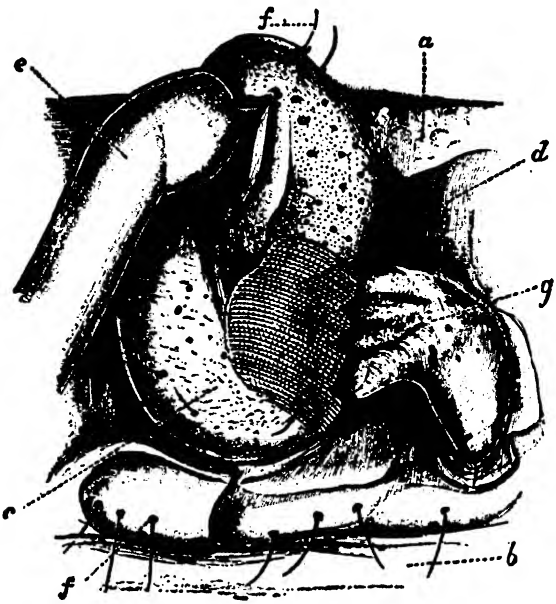

FIG. 103. Stridulating organ of a larva of *Passalus*; *a*, *b*, portions of the metathorax; *c*, coxa of the second leg; *d*, file; *e*, basal part of femur of middle leg; *f*, hairs with chitinous process at base of each; *g*, the diminutive third leg modified for scratching the file. (From Comstock after Sharp)

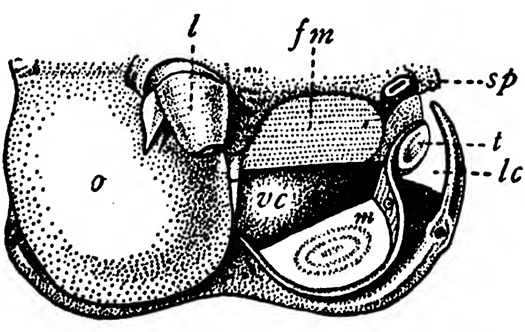

FIG. 104. The musical apparatus of a cicada; *fm*, folded membrane; *l*, base of leg; *lc*, lateral cavity; *m*, mirror; *o*, operculum, that of the opposite side removed; *sp*, spiracle; *t*, timbal; *vc*, ventral cavity. (After Carlet)

102. In other orders, such as the beetles, the scraper and file may be on the leg and body, respectively, fig. 103. It appears in these cases that the body wall itself serves as the vibrating surface. A unique mechanism is developed in the cicadas, fig. 104. They possess a set of membranes situated in ventral pouches or cavities near the base of the abdomen. One of these membranes is connected internally with a muscle fiber. The contraction of this muscle pulls the membrane inward; the relaxation of the muscle allows the membrane to snap back to its original shape. These movements are alternated with great speed to produce sound waves. The other membranes act as sound reflectors.

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4

Internal Anatomy

The internal anatomy of insects involves primarily the organs which carry on the vital functions of life. These organs are protected from outside forces by the body wall. If parts of certain organs project as flaps or lobes beyond the body outline, they are incased by a thin mantle of body wall and are thus within the confines of the exoskeleton.

DIGESTIVE SYSTEM

The digestive system is the food tract and its accessory parts. It is composed of the alimentary canal and various glands connected with it either directly or indirectly. Typically these include the salivary glands, gastric caeca, and Malpighian tubules.

Alimentary Canal, Fig. 105. This organ is an asymmetrical tube passing through the central part of the body. Its anterior opening,

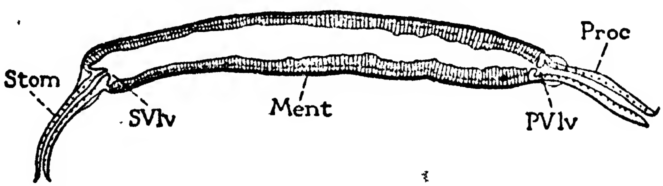

FIG. 105. The alimentary canal of a collembolan *Tomocerus niger,* showing in simple form the primary components of the food tract without secondary specializations. *Ment,* mesenteron; *Proc,* proctodeum; *Pvlv,* proctodeal or pyloric valve; *Stom,* stomodeum; *SVlv,* stomodeal or cardiac valve. (After Snodgrass)

the mouth, is situated at the base of the *preoral cavity* (the space enclosed by the mouthparts); its posterior opening, the *anus,* is on the posterior body segment. The alimentary canal is divided into.

three distinct parts: an anterior *stomodeum,* a middle *mesenteron,* and a posterior *proctodeum.* Usually between the stomodeum and mesenteron is the *stomodeal* or *cardiac valve,* and between the mesenteron and the proctodeum is the *proctodeal* or *pyloric valve.* The stomodeum and proctodeum result from embryonic infoldings of the ectoderm; the mesenteron is formed from the mesoderm; this is discussed further in the portion on embryology.

In a few primitive insects the three parts of the alimentary canal are simple and tubular in shape, fig. 105. In most insects, however,

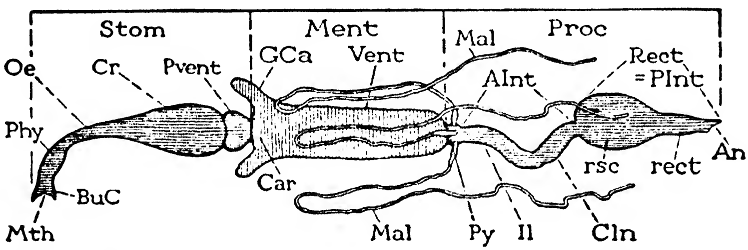

FIG. 106. Diagram showing the usual subdivisions and outgrowths of the alimentary canal. *AInt,* anterior intestine; *An,* anus; *BuC,* buccal cavity; *Car,* cardia; *Cln,* colon; *Cr,* crop; *GCa,* gastric caecum; *Il,* ileum; *Mal,* Malpighian tubules; *Ment,* mesenteron (ventriculus); *Mth,* mouth; *Oe,* oesophagus; *Phy,* pharynx; *PInt,* posterior intestine (rectum); *Proc,* proctodeum; *Pvent,* proventriculus; *Py,* pylorus; *Rect,* rectum (*rect,* rectum proper; *rsc,* rectal sac); *Stom,* stomodeum; *Vent,* ventriculus. (After Snodgrass)

each of these parts has become differentiated into functional subdivisions. The typical structure of these is as follows, fig. 106:

Stomodeum. This portion is usually divided into three main portions: (1) an anterior, more or less tubular portion, the *oesophagus,* followed by (2) an enlarged portion, the *crop,* which narrows to (3) a valvelike *proventriculus* at the junction with the mesenteron. An indefinite portion of the oesophagus at the mouth opening is frequently called the *pharynx* but is difficult to identify without a knowledge of the musculature. The boundary between oesophagus and crop is frequently arbitrary, as in fig. 106; in some insects such as certain moths, fig. 107*C,* the crop is developed into a spherical chamber; this modification is carried still further by many flies, fig. 108, and the crop forms a sack connected to the oesophagus by a long lateral tube. The proventriculus may be a simple valve opening into the mesenteron; in insects which eat solid food, it bears a series of hooks for food shredding and is called the *gastric mill.*

Mesenteron. This middle portion of the alimentary canal is the place where digestion takes place. It is frequently called the *ven-*

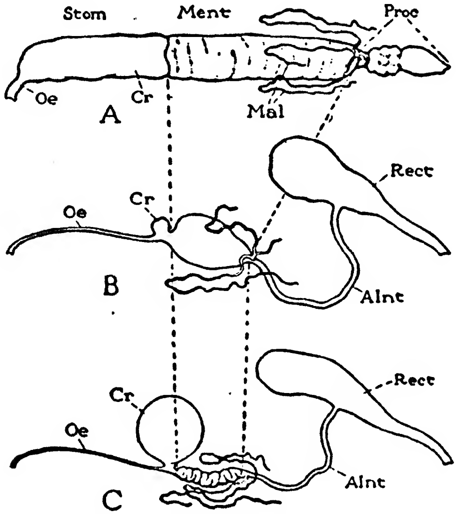

Fig. 107. Transformation of the alimentary canal of a moth *Malacosoma americana,* from the larva, *A,* through the pupa, *B,* to the imago, *C.* Abbreviations as for fig. 106. (After Snodgrass)

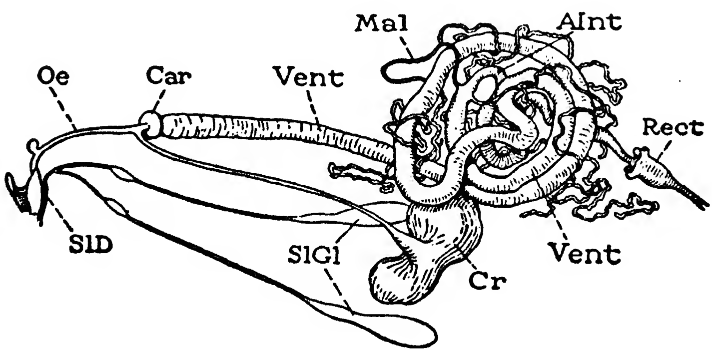

Fig. 108. Alimentary canal and salivary glands of a fruit fly *Rhagoletis pomonella,* showing the diverticular crop (*Cr*) and the cardiac sac (*Car*) of the ventriculus, characteristic of many Diptera. *SlD* and *SlGl,* labial duct and gland; other abbreviations as in fig. 106. (After Snodgrass)

triculus or stomach. Usually it is tubular, but occasionally it is subdivided into definite parts. This subdivided condition is most pronounced in the Hemiptera, in which the mesenteron may have three or four sections. The mesenteron typically bears several finger-like outgrowths, the *gastric caeca.* These usually occur at the anterior end of the stomach, fig. 106, but may be situated on more posterior portions.

Proctodeum. This posterior portion of the alimentary canal varies greatly in different insects but is usually divided into a tubular *anterior intestine* and an enlarged *posterior intestine.* This latter is termed the *rectum* and is connected directly with the anus.

Malpighian Tubules. With few exceptions insects possess a group of long slender tubules branching from the alimentary canal near the junction of the mesenteron with the proctodeum, fig. 106. These are the Malpighian tubules, which are excretory in function. The number of these tubules varies from 1 to 150. When a large number of these are present, they are often grouped into bundles of equal size.

Labial Glands. Most insects possess a pair of glands lying along side the mesenteron, fig. 108, and associated with the labium. Each of these glands has a duct running anteriorly. These unite, usually within the head, to form a single duct that opens into the preoral cavity between the labium and the hypopharynx. The function of these glands differs in various insects and in some has not been determined definitely. In most insects the labial glands secrete saliva, as in cockroaches. In lepidopterous and hymenopterous larvae these glands secrete silk, used in making larval nests and pupal cells. In blood-sucking insects the labial glands secrete an anticoagulin which keeps ingested blood in liquid form.

CIRCULATORY SYSTEM

The circulatory system comprises chiefly the blood and tissues and organs which cause its circulation through the body. In many animals, such as the vertebrates, the blood travels only through special vessels (arteries, capillaries, and veins) developed for this purpose. This condition is called a closed system. In insects this is not the case. For most of its course the blood simply flows through the body cavity or coelom, irrigating the various tissues and organs. There is a special pumping organ or heart situated dorsally in the insect body which pumps the blood from the posterior portion of the body and empties it into the internal cavity of the head. From this cavity the blood again flows back through the body, is drawn into the heart and again pumped forward, and so on. This kind of arrangement is called an *open system.*

Blood. The fluid which circulates through the body cavity is called the blood. It consists of a liquid part, the *plasma* or *hemolymph,* and an assortment of free floating cells, called blood *corpuscles* or

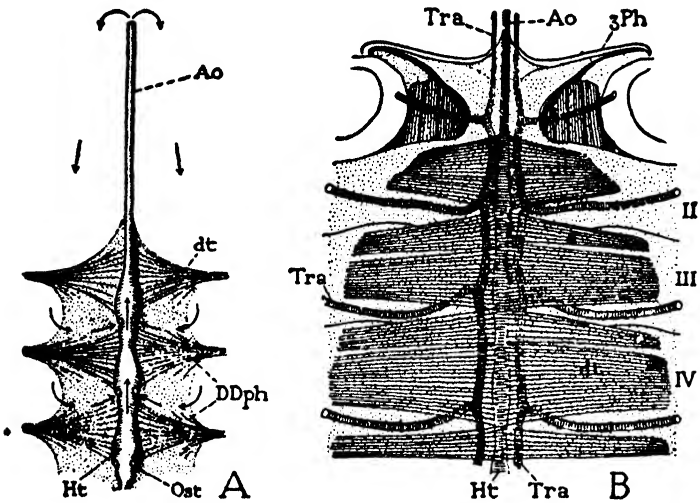

Fig. 109. The dorsal blood vessel and the dorsal diaphragm. *A,* diagram of aorta and three chambers of the heart with corresponding part of the dorsal diaphragm, dorsal view, arrows suggesting the course of blood circulation. *B,* dorsal vessel and dorsal diaphragm of *Dissosteira carolina* from metathorax to fifth abdominal segment, ventral view. *Ao,* aorta; *DDph,* dorsal diaphragm; *dt,* diaphragm muscles; *Ht,* heart; *Ost,* ostia; *Ph,* phragma; *Tra,* trachea. (After Snodgrass)

hemocytes. Study of the blood involves histology and physiology and is discussed in the next chapter.

Dorsal Vessel. As its name implies, the dorsal vessel, fig. 109, lies directly beneath the dorsum, or dorsal body wall. It extends the length of the body, from the posterior end of the abdomen into the head. It is the principal pulsating organ which causes the flow of the blood.

The dorsal vessel is divided into two parts: a posterior portion called the *heart,* and an anterior portion called the *aorta.* In general, the heart is the pulsating portion, and the aorta is the tube which carries the blood forward and discharges it into the head.

The *heart* is more or less swollen in each segment to form segmental *chambers* separated by constrictions. This chambered portion typically consists of nine parts, occurring in the first nine segments of the abdomen. Each chamber has a pair of lateral openings or *ostia*, through which blood enters the chamber. In certain insects the heart may depart radically from this typical condition. In cockroaches and japygids, for example, the first two chambers occur in the meso- and metathorax. In the bug *Nezara* the heart consists of a single large chamber having three pairs of ostia.

The *aorta* is typically a simple tubular extension of the heart. In some forms, such as cranefly larvae, the aorta also pulsates and thus is an accessory to the heart in causing circulation.

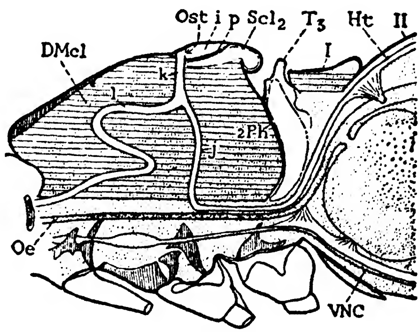

Fig. 110. Vertical section of thorax and base of abdomen of *Sphinx convolvuli*, showing aortic diverticulum (k) and pulsating membrane (p) in mesothorax. *DMcl*, dorsal muscle; *Ht*, heart; *i*, sinus; *j*, *l*, aorta; *Oe*, oesophagus; *Ost*, ostium; *Ph*, phragma; *Scl*, scutellum; *T*, tergite; *VNC*, ventral nerve cord. (After Snodgrass, from Brocher)

Dorsal Diaphragm and Sinus. Connected to the underside of the heart are pairs of muscle bands known as *wing muscles* or *alary muscles*. This name is applied because the muscles form flat fans or wings which connect the heart and the lateral portions of the tergites. These aliform muscles, when well developed, form a fairly complete partition between the main body cavity and the region around the heart. In such cases the partition is called the *dorsal diaphragm*, and the segregated heart region is termed the *dorsal sinus*. The diaphragm and sinus extend only as far as the heart and are not continued forward in the region of the aorta.

Accessory Pulsating Organs. In addition to the heart there may occur other pulsating organs for assisting in blood circulation. The two of most frequent occurrence are the thoracic pulsating organs and the ventral diaphragm. Other accessory structures are found only rarely.

Thoracic Pulsating Organs, Fig. 110. In many insects, especially rapid fliers such as hawk moths, there is a pulsating organ which draws blood through the wings and discharges it into the aorta. The pulsating organ itself is a cavity in the scutellum provided with a flexible or pulsating membrane. The outlet of the structure is a tube called the aortic diverticulum which connects directly with the aorta.

Ventral Diaphragm. Many Orthoptera, Hymenoptera, and Lepidoptera have muscle bands developed *over* the ventral nerve cord in much the same manner as the aliform muscles form a diaphragm *under* the heart, which is dorsal in position. When such a muscle band is formed over the nerve cord, it is known as the ventral diaphragm. By expansion and contraction it produces a flow of blood posteriorly and laterally.

TRACHEAL SYSTEM

Most insects possess a system of internal tubes or *tracheae,* for conducting free air to the cells of the body. This system of tubes is the *tracheal system,* and it performs the function of *respiration.* In almost all other animals respiration is a function of the blood stream, in conjunction with aerating surfaces such as skin or lungs. In addition to insects, however, a few groups of the Arthropoda possess a well-developed tracheal system. These groups include some of the Arachnida, a few Crustacea, and most of the Chilopoda. Rudimentary tracheal tubules are found in Onychophora and Diplopoda.

This tracheal system is of necessity highly complex, because it must branch into a myriad of fine tubules, each of which reaches intimately only a small group of cells. This intricate branching of tracheae in insects is analogous to that of the blood vessels and capillaries in the vertebrates.

Principal Components of Tracheal System

A common type of tracheal system is shown in fig. 111. The tracheae form definite groups in each segment and receive air from the exterior by means of segmentally arranged pairs of openings called *spiracles* (*s*). The spiracles join more or less directly with a main tracheal trunk (*t*), a pair of which usually run the full length of the body. In each segment there arise from these trunks various branches (always paired, since one comes from each trunk) which aerate the tissues of the organs. The number and position of these branches vary greatly in different insects, but generally there are three large branches given off on each side in any one segment: (1) a dorsal branch aerating the dorsal vessel and dorsal muscles, (2) a ventral or visceral branch aerating the digestive and reproductive organs, and (3) a ventral branch aerating the ventral muscles and nerve cord.

The fine tips of the tracheae divide into minute capillary tubes, or tracheoles, usually one micron or less in diameter. These tracheoles ramify between and around cells of other tissues and are the functional part of the system through which oxygen diffuses into the body cells.

Tracheal Trunks. The segmental arrangement of clusters of tracheal branches indicates that originally insects had an independent tracheal system in each postoral segment, with no connection between tracheae of different segments. With only few exceptions, however, insects of the present have connections between the tracheae of adjoining segments if the tracheal system is developed. These connecting tubes form trunks. In many insects the main tracheal trunks are lateral in position and are called the *lateral tracheal trunks.* Frequently a second pair of *dorsal tracheal trunks* are found, one on each side of the heart. These are usually small in diameter and secondary to the lateral trunks. In most fly larvae the opposite is the case. There the dorsal trunks are greatly developed and are the chief respiratory passages, fig. 112.

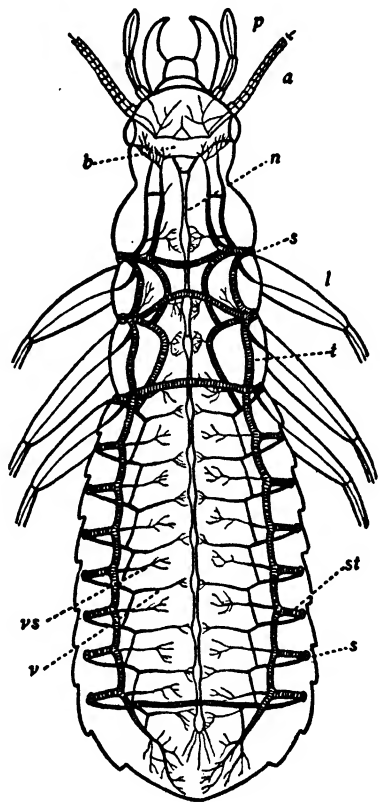

FIG. 111. Tracheal system of an insect. *a*, antenna; *b*, brain; *l*, leg; *n*, nerve cord; *p*, palpus; *s*, spiracle; *st*, spiracular branch; *t*, main tracheal trunk; *v*, ventral branch; *vs*, visceral branch. (From Folsom, after Kolbe)

Tracheal Air Sacs. An important feature in many groups is the development of air sacs that serve as air-storage pockets to aid respiration. These are often enlargements of the tracheal trunks, as in fig. 113. In many fast-flying insects, such as the housefly and the bees, the sacs fill a large part of the body cavity. These sacs can be squeezed and released by muscular contraction of the body to act like bellows and increase intake and expulsion of air.

Spiracles. When functional, spiracles are an important control over respiration. They are extremely varied in size, shape, and structure.

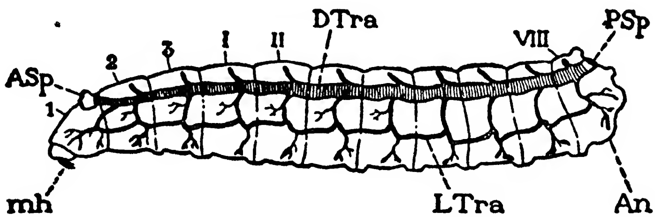

FIG. 112. Fly larva illustrating large dorsal tracheal trunks. *An,* anus; *ASp,* anterior spiracle; *DTra,* dorsal tracheal trunk; *LTra,* lateral tracheal trunks; *mh,* mouth hooks; *PSp,* posterior spiracles. (After Snodgrass)

If functional, they all have some sort of closing device. This device may be *external* (usually in the form of two opposed lips), or it may be *internal* (usually in the form of a clamp which pinches the trachea shut).

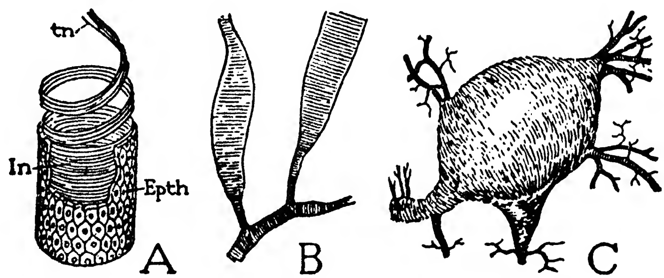

FIG. 113. Structure of a tracheal tube, *A,* and examples of tracheal air sacs, *B, C.* *Epth,* epithelium; *In,* intima; *tn,* taenidium in spiral band of cuticular intima artificially separated. (After Snodgrass)

Open Tracheal Systems

Systems in which spiracles are open and functional are called open systems. The more generalized type has ten pairs of spiracles, a pair on the mesothorax, metathorax, and each of the first eight abdominal segments. Many modifications of this type occur, including such examples as mosquito larvae, having spiracles on only the eighth abdominal segment; most of the maggots, which have only prothoracic spiracles and the terminal pair on the eighth abdominal segment;

fly pupae, which have only the prothoracic spiracles; several aquatic forms, such as the rat-tailed maggots, having the posterior spiracles on a long extensile tube which is exserted through the breeding medium into the air.

Closed Tracheal Systems

In many forms of insects the spiracles are either functionless or entirely absent. In these cases the tracheal system is termed *closed.* It is usually well developed otherwise, as concerns the tracheal trunks and their interior branches. In most closed systems the spiracles are replaced by a network of fine tracheae which run under the skin or into gills. This is illustrated by nymphs and larvae of many aquatic insects, such as mayflies, stoneflies, and damselflies.

An interesting modification among the aquatic insects occurs in dragonfly nymphs. In these the rectum contains internal gill-like folds. Fine tracheae extend throughout these folds. The nymph periodically draws water into the rectum, and expels it, bathing these *rectal gills* and thus aerating the tracheae in them.

NERVOUS SYSTEM

The nervous system in insects is highly developed and consists of a central system and a stomodeal system. As in other animals, the nervous system serves to coordinate the activity of the insects with conditions both inside and outside the body.

Central Nervous System. The basic units of the central nervous system, fig. 114, are essentially: (1) the brain, situated in the head, and (2) paired nerve centers or *ganglia,* one ganglion in each segment. The ganglia are connected by double fibers into a cord, and the anterior ganglion is connected with the brain. Concurrently with the fusion of body segments which occurred in the evolution of the insect group, fig. 13, there occurred also a fusion of the ganglia belonging to each segment. For this reason the nerve centers in the head bear little apparent resemblance to the primitive condition, for the head is in reality composed of the archaic head, or prostomium, plus four body segments which join with it to make a solid mass.

Brain. The brain, fig. 115, is situated in the head above the oesophagus and for this reason is frequently referred to as the *supraoesophageal ganglion.* It has three principal divisions: (1) the

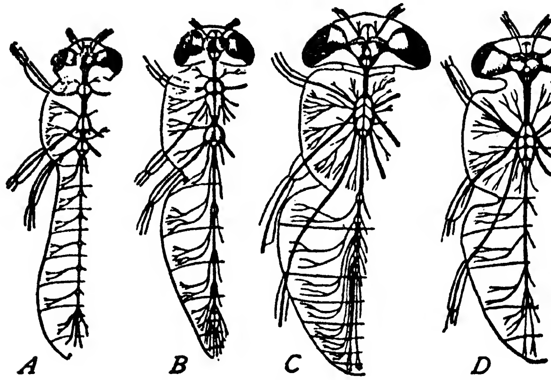

FIG. 114. Successive stages in the concentration of the central nervous system of Diptera. *A, Chironomus; B, Empis; C, Tabanus; D, Sarcophaga.* (From Folsom and Wardle, after Brandt)

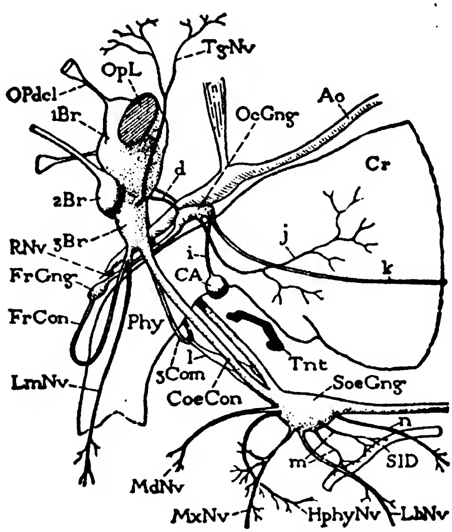

FIG. 115. Brain and associated structures of a grasshopper, lateral view. *Ao,* aorta; 1 *Br,* protocerebrum; 2 *Br,* deutocerebrum; 3 *Br,* tritocerebrum; *CA,* corpus allatum; *CoeCon,* circumoesophageal connective; 3 *Com,* tritocerebral commissure; *Cr,* crop; *FrCon,* frontal ganglion connective; *FrGng,* frontal ganglion; *HphyNv,* hypopharyngeal nerve; *LbNv,* labial nerve; *LmNv,* labral nerve; *MdMv,* mandibular nerve; *n,* cervical nerve; *OcGng,* occipital ganglion; *OPdcl,* ocellar pedicel; *OpL,* optic lobe; *Phy,* pharynx; *RNv,* recurrent nerve; *SlD,* salivary duct; *SoeGng,* suboesophageal ganglion; *TgNv,* dorsal tegumentary nerve. (After Snodgrass)

protocerebrum which innervates the compound eyes and ocelli, (2) the *deutocerebrum* which innervates the antennae, and (3) the *tritocerebrum* which controls the major sympathetic nervous system. All three of these parts are definitely paired.

In its long evolutionary development, the various parts of the insect head have shifted somewhat in general orientation. Because of this shifting, the brain, which was originally *in front of* the mouth, is now *above* the mouth or oesophagus. The protocerebrum and deutocerebrum are situated above the oesophagus and for this reason are considered to be the outgrowth of the primitive prostomial brain such as is found in the annelids. The tritocerebrum is intimately joined with the deutocerebrum, but its two halves are connected by a commissure or connective fiber which passes *underneath* the oesophagus. For this reason it is thought to be the ganglion of the first true body segment, now fused with the head.

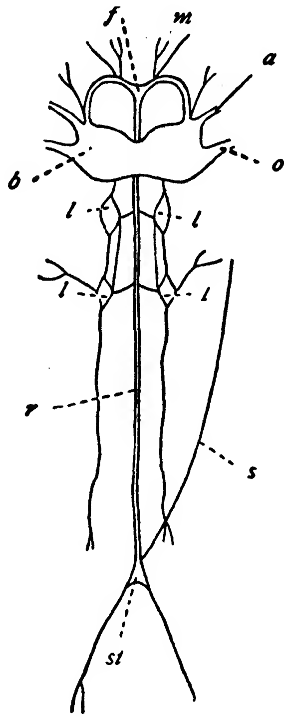

FIG. 116. Sympathetic nervous system of an insect, diagrammatically represented. *a*, antennal nerve; *b*, brain; *f*, frontal ganglion; *l*, *l*, paired lateral ganglion; *m*, nerves to upper mouthparts; *o*, optic nerve; *r*, recurrent nerve; *s*, nerve to salivary glands; *st*, stomachic ganglion. (From Folsom and Wardle after Kolbe)

Suboesophageal Ganglion. Situated in the head, beneath the oesophagus and joined to the brain by a pair of large connectives, is a large nerve center, the suboesophageal ganglion. It is in reality the fused ganglia of the original mandibular, maxillary, and labial segments. This composite ganglion gives rise to the nerve trunks servicing the mouthparts. From this nerve center a pair of connectives pass through the neck into the thorax.

Ventral Nerve Cord. In the thorax and abdomen there is typically a nerve ganglion in the ventral portion of each segment. The ganglia of adjoining segments are joined by paired connectives, the whole forming a chain of nerve centers stretching posteriorly from the prothorax, fig. 114. This chain is the ventral nerve cord. It is joined to the suboesophageal ganglion by the connective passing through the neck. The thoracic ganglia give rise to the nerves controlling the legs and wings, and the abdominal ganglia have branches and fibers to the abdominal muscles and abdominal appendages.

The generalized ventral nerve cord is composed of a chain of well-separated ganglia. In various groups of insects certain of these may fuse to form a smaller number of larger units. This type of modification is demonstrated strikingly in the order Diptera, fig. 114. Primitive members of this order possess a fairly generalized nerve cord; in more specialized families the thoracic ganglia fuse into a single large mass, and the abdominal ganglia become smaller and finally are scarcely discernible. The stages in this series of modifications are shown in fig. 114, *A* to *D*.

Stomodeal Nervous System. To control some of the "involuntary" motions of the anterior portions of the alimentary tract and dorsal blood vessel, insects possess a so-called "sympathetic" nervous system, fig. 116. There is considerable doubt, however, as to the exact function of many branches. It is more appropriate to term it the stomodeal system, because most of the parts are situated on the top or sides of the stomodeum. The central structure of this stomodeal system appears to be the *frontal ganglion,* which is situated in front of the brain and connected with the tritocerebrum by a pair of fibers. From the frontal ganglion a median recurrent nerve runs back beneath the brain and along the top of the oesophagus, where it connects with a system of small ganglia and nerves. This group innervates the stomodeum, salivary ducts, the aorta, and apparently certain muscles of the mouthparts.

MUSCULATURE

The insect body is provided with an extremely complex system of muscles. These are responsible for almost all the movements of the body and its appendages. Some insects may possess over two thousand muscle bands.

In a dissection, muscle tissue is one of the conspicuous features within the insect body. It does not form a continuous system but is distributed in different areas and enters into the composition of several organs. On the basis of distribution, muscle tissue may be grouped into three categories.

Visceral Muscles. The digestive tract and ducts of the reproductive system have an outer layer of muscle, which produces peristaltic move-

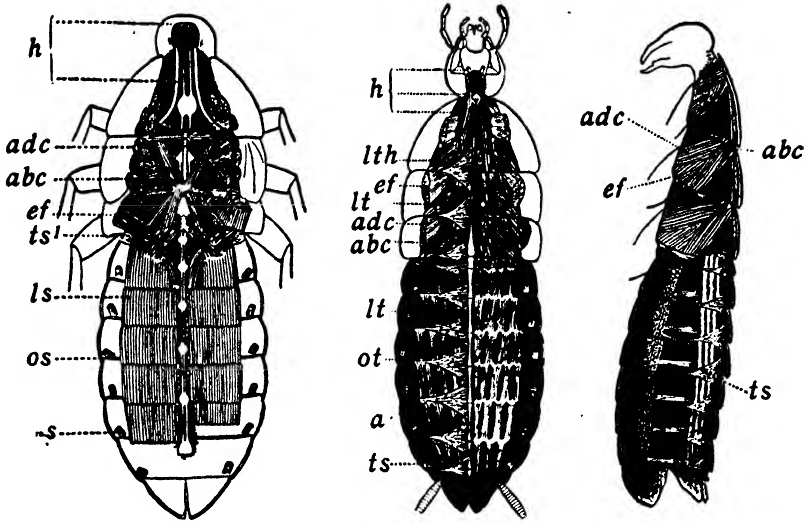

FIG. 117. Body musculature of a cockroach, showing ventral, dorsal and lateral walls, respectively. *a*, alary muscle; *abc*, abductor of coxa; *adc*, adductor of coxa; *ef*, extensor of femur; *h*, head muscles; *ls*, longitudinal sternal; *lt*, longitudinal tergal; *lth*, lateral thoracic; *os*, oblique sternal; *ot*, oblique tergal; *ts*, tergosternal; *ts*, first tergosternal. (From Folsom and Wardle, after Miall and Denny)

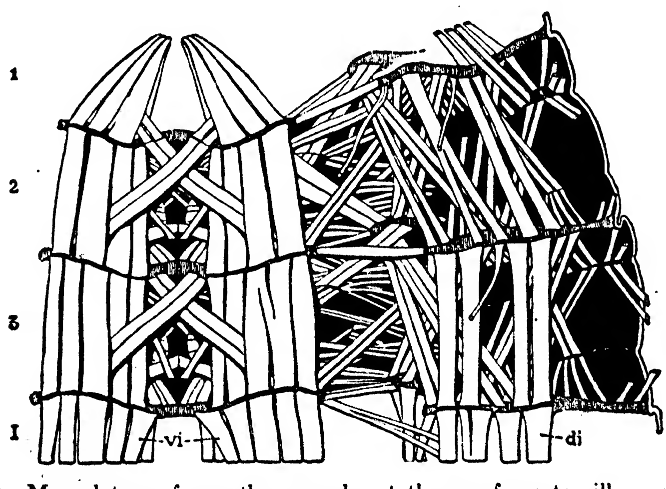

FIG. 118. Musculature of mesothorax and metathorax of a caterpillar. *di*, dorsal bands; *vi*, ventral bands. (After Snodgrass)

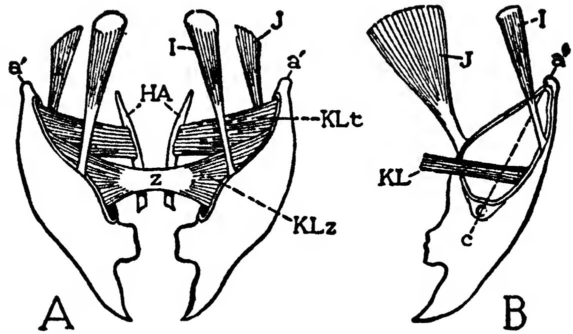

FIG. 119. Diagram of the mandibular muscles of insects. *A*, apterygote type with one articulation, *a'*; *B*, pterygote type with two articulations, *a'*, *c*. Homologous muscles are lettered to match. (After Snodgrass)

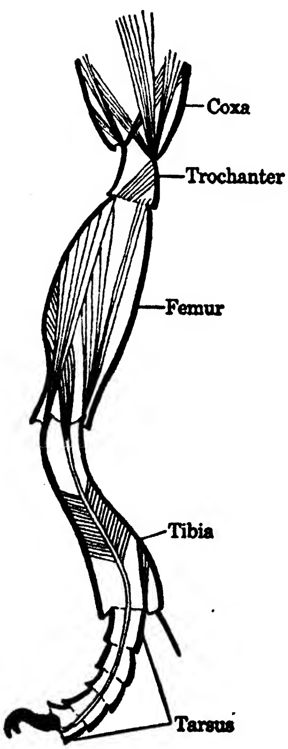

FIG. 120. Diagram of an insect leg and its musculature. (Adapted from Berlese)

ments. The muscle may be in circular, longitudinal, or oblique bands, or a combination of these. Special muscles occur in such places as the closing or opening mechanism of spiracles and in the mouth region. Muscles form pulsating bands which assist in the operation of the circulatory system.

Segmental Bands. The various segments of the body are connected by series of muscle bands which maintain body form, fig. 117. In the abdomen, the tergites are connected by longitudinal dorsal bands, and the sternites are connected by longitudinal ventral bands. The tergite and sternite of the same segment are connected by oblique or perpendicular tergosternal muscles. In the thorax the musculature appears entirely different. The most conspicuous muscles are large cordlike groups which operate the legs and wings; the other muscles are subordinate to these in size and prominence. In addition to these major muscle groups, there are many smaller bands which may be extremely complicated in pattern, fig. 118. In both thorax and abdomen the exact muscle pattern differs markedly in various kinds of insects.

Muscles of the Appendages. The movable appendages have muscle bands of varying size and complexity. The mandibles of chewing insects have a few muscle groups which fill a large portion of the head capsule, but there are no muscles within the mandible itself, fig. 119. On the other hand, appendages which are divided into segments, such as the maxillae and legs, fig. 120, not only are activated by the large muscles inside the body, but in addition have muscles extending from segment to segment.

REPRODUCTIVE SYSTEM

Insects are primarily dieceous, in that normally only one sex is represented in any one individual. A few rare instances are known of hermaphroditic insects in which both sexes are represented in the

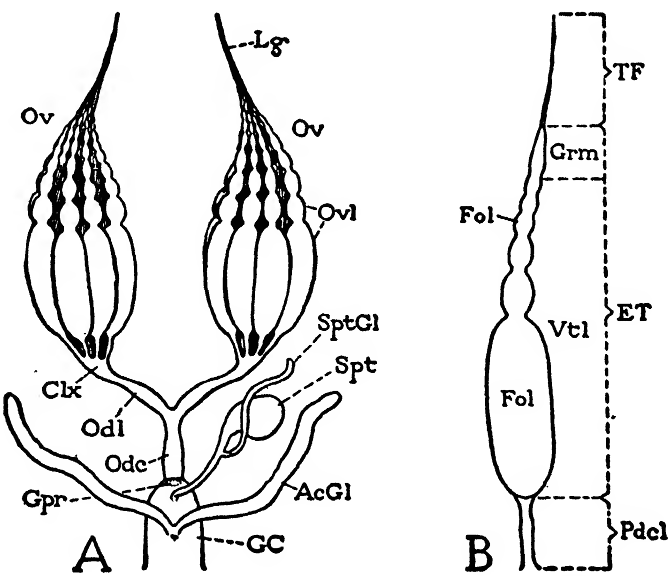

Fig. 121. Typical female reproductive system of an insect. *A*, diagram of the ovaries, exit ducts, and associated structures. *B*, diagram of an ovariole. *AcGl*, accessory gland; *Clx*, calyx; *ET*, egg tube; *Fol*, follicle, or egg chamber; *GC*, genital chamber (vagina); *Gpr*, gonopore; *Grm*, germarium; *Lg*, ovarial ligament; *Odc*, oviductus communis; *Odl*, oviductus lateralis; *Ov*, ovary; *Ovl*, ovariole; *Pdcl*, ovariole pedicel; *Spt*, spermatheca; *SptGl*, spermathecal gland; *TF*, terminal filament; *Vtl*, vitellarium. (After Snodgrass)

same individual. The most notable case is the cottony cushion scale, *Icerya purchasi.*

In insects the reproductive system is a highly developed set of organs situated in the abdomen. There is a close parallel between the parts of the male and female systems, and most parts of both are bilaterally symmetrical.

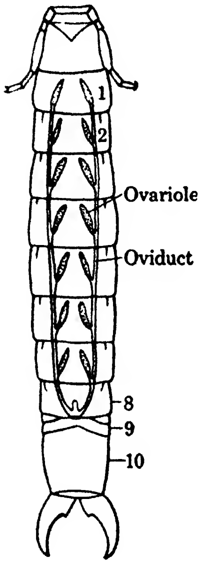

FIG. 122. Female reproductive system of *Heterojapyx gallardi.* (Redrawn from Snodgrass)

Female Reproductive System. The female system consists essentially of a group of ovaries in which the eggs are produced, a spermatheca in which sperms are stored, and a duct arrangement through which the eggs are discharged outside the body. A typical system is illustrated in fig. 121. There are two ovaries, one on each side of the body. An *ovary* consists of several to many *ovarioles* or tubules. Each ovariole ends in an attachment thread, called the terminal filament; the upper part of the ovariole contains the forming eggs and the lower larger portion contains the more matured eggs; the bottom of the ovariole forms a small duct or pedicel. The pedicels of each group unite to form a *calyx.* Each calyx opens into a lateral oviduct. The oviducts of the two sides join to form a common *oviduct.* This opens into an egg-holding chamber, or *vagina,* which opens directly into the external ovipositor, or egg-laying mechanism.

Two glands are connected with the dorsal wall of the oviduct. One is the *spermatheca,* a single bulbous organ with a gland attached to its duct. The other is a paired structure, the *accessory glands* or *colleterial glands,* which secrete adhesive material used in making a covering over egg masses or gluing eggs to a support.

In some of the more primitive groups such as the Orthoptera, the vagina may be only a pouchlike invagination of the eighth sternite.

Many deviations are found from the system just described with differences occurring in the number and shape of ovaries and tubules, ducts, and glands. In many groups the spermatheca exhibits many shapes which are of considerable taxonomic value.

The primitive family Japygidae has a most interesting reproductive system. The ovarioles, fig. 122, are arranged segmentally, linked together by a pair of long lateral oviducts which fuse to form a single oviduct near the egg-laying aperture. This condition suggests that the ancestral insect groups possessed independent ovaries in each segment and that there has occurred a constant migration and consolidation of these to the posterior end of the body, evolving finally the typical system shown in fig. 121.

Male Reproductive System. In general organization the male system is similar to the female. It consists primarily of a pair of testes, associated ducts and sperm reservoirs, and outlets to the outside of the body. A common type is shown in fig. 123.

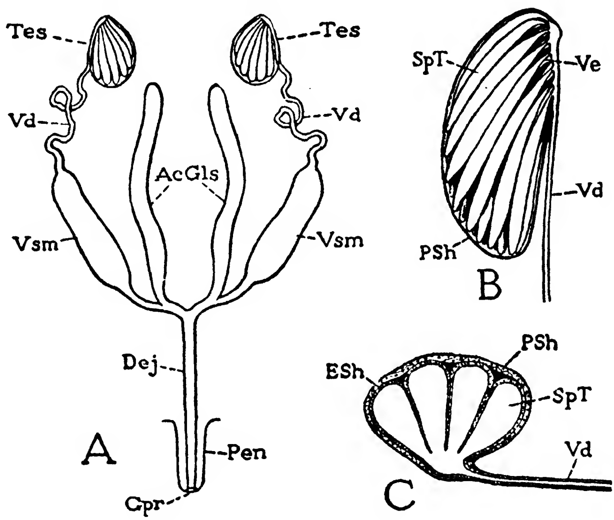

FIG. 123. Typical male reproductive system of an insect. *A*, the male reproductive system. *B*, structure of a testis. *C*, section of a testis and duct. *AcGls*, accessory glands; *Dej*, ductus ejaculatorius; *ESh*, epithelial sheath; *Gpr*, gonopore; *Pen*, penis; *PSh*, peritoneal sheath; *SpT*, spermatic tube; *Tes*, testis; *Vd*, vas deferens; *Ve*, vas efferens; *Vsm*, vesicula seminalis. (After Snodgrass)

Each testis consists of a group of *sperm tubes*, in which the sperms are produced. The sperm tubes open into a common duct, the *vas deferens*, which in turn opens into a reservoir, the *seminal vesicle.* From each seminal vesicle proceeds a duct, the two ducts joining to form a common ejaculatory duct. This duct runs through the penis, at the end of which is the sperm escape opening. The penis is usually associated with structures of the external male genitalia; the structure called the *aedeagus* usually forms a rigid sheath around the true membranous penis. Associated with the internal part of the ejaculatory duct are *accessory glands,* which may be single or paired.

SPECIALIZED TISSUES

In addition to the extensive systems outlined in the preceding pages, the insect body contains some other smaller or less definitely organized tissues. The most important are the *fat body,* the *enocytes,* and the *corpora allata.*

The Fat Body. This is a loosely organized aggregation of cells which occurs throughout the body, especially in the later larval or nymphal instars. The cells of the fat body may be packed so tightly as to appear like an organized tissue. The function of this fat body is partly to store food and partly to aid in excretion.

Enocytes. These are clusters of cells or single large cells which occur at various points in the body cavity. Their function is not yet demonstrated satisfactorily.

Corpora Allata. These are a pair of ganglia-like bodies, fig. 115, closely associated with the stomodeal nervous system. Their full function is obscure, but they are known to secrete hormones.

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Snodgrass, R. E., 1935. Principles of insect morphology. New York, McGraw-Hill Book Co., Inc. 667 pp., illus.

5

Physiology

The physiology of insects has been a neglected field of study until comparatively recent years. In the last decade it has received great impetus because of the importance of knowing more about the physiological processes in insects as a means to further advances in methods of insect control.

This chapter deals primarily with the functions of the organs and tissues. In order to understand these functions, it is necessary to have a general idea of the morphology of the insect body and also detailed information regarding the cellular structure of the organ or tissue involved. Internal anatomy is especially important, and its general outlines should be mastered before physiology is studied. Because the processes of organ physiology rest on cell physiology, it has seemed practical to combine the discussion of physiology with that of histology.

Most if not all of the basic chemical and physical processes involved in insect physiology are the same as those occurring in other forms of animal life. These include such items as the oxidation of foods in metabolism, oxygen and carbon dioxide exchange in respiration, fertilization in reproduction, and the transmission of an impulse over a nerve fiber. Some of the more gross processes, such as molting and the character of the integument, are more peculiar to insects and their allies. It is this type of process which is stressed in this chapter.

BODY WALL; INTEGUMENT

The body wall is the surface layer of ectoderm which surrounds the body and appendages. It is a complex organ, not only being composed of the surface covering or integument, but also containing many kinds of external hairs and sense receptors and internal processes of many types for attachment of muscles.

The body wall has three primary functions: (1) the protection of the organism from outside forces, such as evaporation (insects' most important enemy), inimical organisms, and disease; (2) the reception of external stimuli through specialized sensory hairs, processes, or areas; and (3) acting as the agent of the locomotor system, since the motivating muscles of the legs, wings, and movable sclerites are attached to the exoskeleton. In addition, the integument cannot stretch and in immature insects must be shed regularly to allow growth. These functions are accomplished by a surprisingly simple cellular structure.

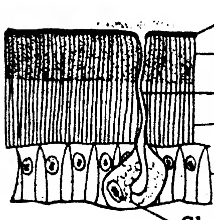


FIG. 124. Diagram of body wall structure. (Adapted from Wigglesworth)

Evaporation. Loss of water by evaporation is the greatest threat to terrestrial organisms, and all insects are terrestrial or aerial for at least some portion of their lives. Evaporation is a function of surface, not volume, and, as size decreases, the ratio of surface to volume increases. Thus insects, being both small and terrestrial, are faced with a major problem of protecting from excessive evaporation the small total amount of water contained in their bodies. The protection lies in the impermeable nature of the insect cuticle, which is remarkably resistant to the passage of water or water vapor. Without such efficient protection it is doubtful if an insect flying in the air, for even a short time, could escape desiccation to a fatal point.

Structure of Integument. The body wall, fig. 124, consists primarily of a layer of cells, the *epidermis,* and a non-living covering, the *cuticle,* which lies on top of and is secreted by the epidermis. Formation of cuticle is the chief function of the epidermis. The cuticle forms a mechanical outer protective layer whose properties contain the key to much insect physiology.

Epidermis. The cells comprising most of the epidermis are simple in type, with large nuclei, united by an indistinct basement membrane. Certain cells of this layer, however, are highly specialized and produce hairs and other surface structures of peculiar types.

Cuticle. The cuticle is made up of a relatively thick inner layer, the *endocuticle,* and a very thin outside *epicuticle.*

The epicuticle is only about a micron thick but seems to be the layer which gives the entire cuticle its property of impermeability. It is composed of *cuticulin,* which is thought to be a mixture of various fats and waxes and which is very similar to the thin outer layer of plant cuticle. The epicuticle contains neither chitin nor protein.

The endocuticle is composed of *chitin* and an insoluble protein. It is flexible, soft, and relatively permeable to water and many substances in aqueous solution. Chitin, the distinctive component of the endocuticle, is susceptible to some acids but is resistant to alkalis. The upper portion of the endocuticle may be differentiated as a more or less definite third layer, the *exocuticle.* This is often impregnated with cuticulin, and color substances, such as carotin and melanin. These substances strengthen and color the soft chitin and give the impregnated areas hardness and much greater impermeability. Such strengthened areas are called "sclerotized" and may contain as little as 20 per cent chitin. Soft areas, which may consist of as much as 80 per cent chitin, are called "membranous."

The endocuticle and exocuticle have the form of a fairly elastic jelly, traversed by extremely fine openings or pore canals. The pore canals run from the epidermal cells to, but not through, the epicuticle. They are believed to be filled with cytoplasmic filaments, which, if it is true, would endow the cuticle with a certain amount of sensitivity. In very thick hard cuticle, as on the elytra of beetles, the cuticle may be laid down as successive series of minute parallel rods, which give the structure additional strength.

Specialized Cells. Certain of the epidermal cells have special functions, either the secretion of fluids or the formation of definite structures such as hairs.

Dermal Glands. Single epidermal cells or groups of cells develop into large cells which produce various secretions. These cells, fig. 124, are connected to the exterior by a duct running through the cuticle. Secretions of different types are produced by a variety of these dermal glands, including wax (often forming definite external patterns), many types of ill-smelling scent compounds, and irritating skin poisons.

Setae, Fig. 125. Most of the flexible hairs or bristles of insects are formed by epidermal cells called *trichogen cells.* At the time of the actual formation of the hair, the trichogen cell is large and nucleated and has a duct which passes through the cuticle to the surface. From this point the products of the cell build up the hair. Closely associated with the trichogen cell is a *tormogen cell,* which forms a socket (usually flexible) around the base of the hair. A hair or bristle of this histological origin is called a *seta* (pl., *setae*). The parent cells may degenerate after the seta is formed.

Specialized setae originate in the same manner. These include scales, poison hairs, and sensory setae.

Color. The great majority of insect colors are located in the epidermis or its vestiture. Insect colors are of two types: pigments and structural colors.

Pigments such as carotin and melanin are deposited in the exocuticle and produce different colors by selective action on different wavelengths of light. These pigments are responsible for practically all non-metallic insect colors and a few metallic ones.

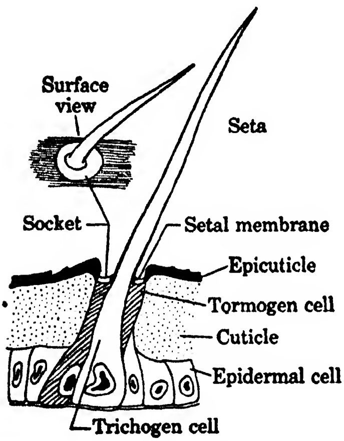
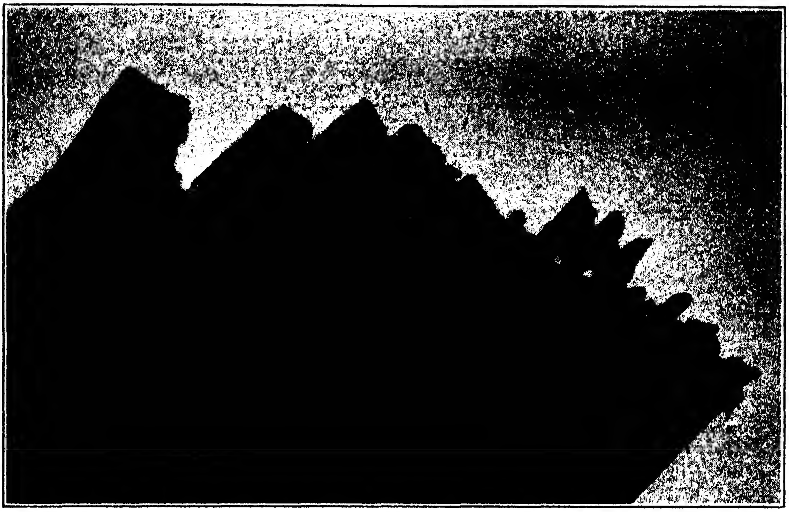


FIG. 125. A seta and its socket. (Adapted from Snodgrass)

Structural colors are produced by extremely delicate and minute vanes which break up light into various wavelengths by reflection and interference. These vanes may be produced by the epicuticle, as is the case with many beetles, especially those with metallic colors. The most common example of this occurs in the moths and butterflies. In these the wings are covered with scales (modified setae), and the scales bear ribs running the length of the scale, fig. 126. Recent studies with the electron microscope have shown that each rib is composed of several parallel extremely thin fenestrate vanes. Studies on the tropical *Morpho* butterflies indicate that ribs of more simple structure produce non-metallic colors and that ribs of great complexity, fig. 127, produce the dazzling iridescent colors for which these butterflies are famous.

Molting. Although in immature insects the cellular epidermal layer of the body wall can grow and expand, the cuticle does not grow or stretch. To allow increase in body size, therefore, an insect must produce periodically a larger new cuticle and shed the old. This phenomenon of shedding the old "skin" is termed *molting* or *ecdysis*. It is one of the most important physiological processes of insects.

The actual shedding of the skin is preceded by a coordinated activity of the epidermal cells and specialized molting glands. There is



A

B

FIG. 126. An iridescent scale of a butterfly wing, photographed with the electron microscope. The pictures are of fractured ends of broken scales to obtain different views of the surface vanes. *A*, ×6000; *B*, ×12,000. (After Anderson and Richards)

some question as to the exact manner in which each step is taken in this process, but the following procedure, fig. 128, seems the best substantiated.

1. The first step is the secretion by the epidermal cells of a new epicuticle under the old endocuticle. This new epicuticle is apparently quite impervious to the molting fluid.

2. The molting glands (which are specialized epidermal cells) enlarge at this time and discharge a *molting fluid* through a duct which

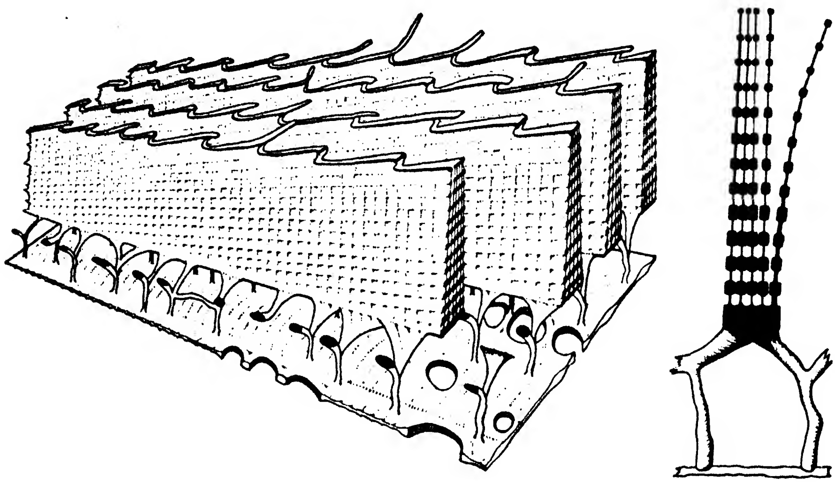


Fig. 127. Diagram of light breaking structure of ribs of butterfly scale shown in fig. 126. × cir. 18,000. (After Anderson and Richards)

opens through and above the new epicuticle. This molting fluid is actually an enzyme which digests protein and chitin, but does not affect cuticulin and the other substances which make up epicuticle and exocuticle. This fluid begins to dissolve away the old endocuticle, which is composed chiefly of chitin.

3. While the molting fluid is dissolving the old endocuticle, the epidermal cells are forming a new one, which is protected from the molting fluid by the new epicuticle. Indications are that both new epicuticle and endocuticle are permeable to the dissolved products resulting from the digestion of the old cuticle, and these products are continually reabsorbed by the epidermal cells. As much as 85 per cent of the old cuticle may be dissolved and presumably used again in the secretion of the new. In this process a space is left between the two cuticles.

4. When the new cuticle is fully formed, the insect has to break out of the old one. The initial rupture is made along a mesal line of weak cuticle which typically extends along the dorsum of the thorax. This rupture is caused by the pressure of the blood. The insect contracts the abdomen, forcing the blood into the thorax and causing it to bulge until the cuticle breaks along the line of weakness. The insect may swallow air (or water, if aquatic) to aid in this process.

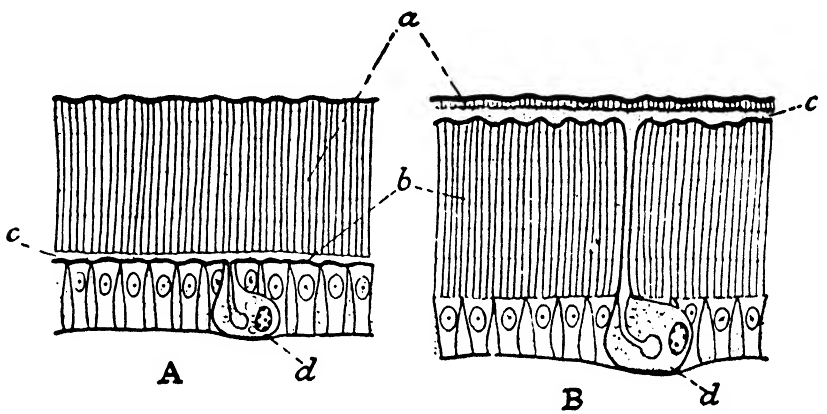


FIG. 128. Diagram of the production of new cuticle prior to molting. *A*, a new epicuticle formed; digestion of old endocuticle scarcely begun. *B*, digestion and absorption of old endocuticle almost complete. *a*, old cuticle; *b*, new cuticle; *c*, molting fluid; *d*, molting gland. (From Wigglesworth, "Principles of Insect Physiology," by permission of E. P. Dutton and Co.)

The insect then wriggles and squirms free from the old skin. At or before this time, the molting fluid is usually reabsorbed by the body, so that at the time of molting the area between the old and new skins may be dry.

5. For a short period after molting the new cuticle can be stretched, at least in the non-sclerotized (membranous) portions. During this short period, therefore, the insect stretches the cuticle to accommodate expected size increase of the body before the next molt. This is done by increasing the blood pressure in first one region and then another, thus "blowing up" the regions and stretching the integument. When the blood pressure is reduced, the stretched integument *does not shrink again* but contracts into a series of small folds or minute accordion-like pleats. In larvae with no sclerotized body areas, these folds may occur over the entire body, fig. 129. In insects with definite sclerotized plates, the folds occur in the membrane between the

sclerites. As the body increases in size with subsequent growth, the integument increases by a simple expansion of the folds, as in figs. 54 and 55. When this avenue for increase is exhausted, the insect must molt again to allow further size increase. The entire active molting process may take only a few seconds, or it may require an hour or more.

6. After its complete formation, the new skin becomes impermeable to many substances, especially water, and is locally sclerotized and colored to assume its normal condition. In many groups, such as the grasshoppers, this occurs just after the stretching process which follows molting. In other cases, for instance in adult Trichoptera, and many Hymenoptera, this occurs before molting while the adult is still incased in the pupal skin. It was thought formerly that hardening and coloring of the skin were a result of its exposure to air after molting. Recent experiments on partial dissection, supplemented by more complete observations on the insect in nature, show that this change is probably caused by direct action of the epidermal cells on the cuticle.

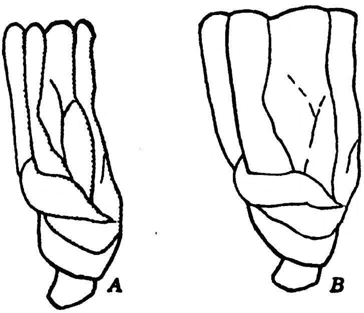


FIG. 129. Abdominal segment of a sawfly larva, showing membranous folds. *A*, immediately after molting; *B*, after growth and expansion.

DIGESTION

Digestion is the process of dissolving and chemically changing food so that it can be assimilated by the blood and furnish nutriment to the body. The food of different insects includes a vast array of material, including living and dead plants, wood, fungi, plant juices, blood, flesh, insects, and practically every other kind of organic matter. As a consequence, many modifications are found in the digestive systems, each adapted to the problem of handling a particular type of food. The digestive system may be entirely different in larval and adult stages of the same insect, fig. 107, especially in such forms as the Diptera, in which the food of the various stages is entirely different. Within an order there may be strikingly different digestive systems. The Hymenoptera, for instance, include such diverse forms as sawfly larvae which are herbivorous and wasp larvae which are internal parasites, each having a different type of digestive system.

A generalized type of digestion and digestive system is found in herbivorous and omnivorous insects such as cockroaches, grasshoppers, and many beetle larvae and adults. This type is used as a basis for the following account. A few of the more conspicuous modifications from this type are discussed; the enormous number of other modifications must be relegated to a specialized study of the subject.

Salivation. In a great variety of insects saliva is mixed with the food before it is ingested. In chewing insects the saliva is ejected into the mouth and mixed with the food there. In sucking insects the saliva is ejected into the liquid food, and the mixture is then siphoned into the pharynx. The saliva is usually produced by the labial glands.

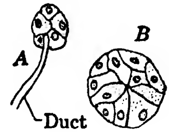


Fig. 130. Acini of salivary gland of a cockroach. *A,* small acinus with duct; *B,* cross section of acinus.

Typically each gland is like a long bunch of grapes, each "grape" a small cluster or *acinus* of secreting cells. Each acinus has its own duct; these join successively to form the large duct of the whole gland. The acinus may contain cells of different histological structure. The labial glands having a function connected with food may be segregated into two general groups, based on the principal substance they are known to secrete.

1. Digestive Group. In many insects the labial glands are the chief source of amylase. This is usually secreted into the food mass before it is swallowed, and the actual digestion takes place in the digestive tract. In adult Lepidoptera and bees the glands secrete invertase, which is exuded at the tip of the proboscis and drawn up into the stomach with the nectar. The enzymes are secreted in the acini, fig. 130. In the cockroach the acini are composed of two types of cells similar in histological and staining characteristics to the chief and parietal cells (secreting pepsin and hydrochloric acid, respectively) of mammalian gastric glands. This apparent homology suggests that the large cells of the acini produce the amylase, and that the small parietal-like cells may secrete some other substance such as an acid.

2. Anticoagulin Group. The labial glands of blood-sucking insects secrete no digestive enzymes but instead produce an anticoagulin. The purpose of this is to prevent the ingested blood meal from clotting and plugging up the beak and digestive tract.

Extraintestinal Digestion. In special cases digestive enzymes are extruded from the body onto or into the food and effect at least partial digestion before the food is taken into the digestive tract. This is called extraintestinal digestion. Plant lice, for instance, extrude saliva containing amylase from the beak into the host tissues and in this way digest starch in the host plant cells. Many predaceous

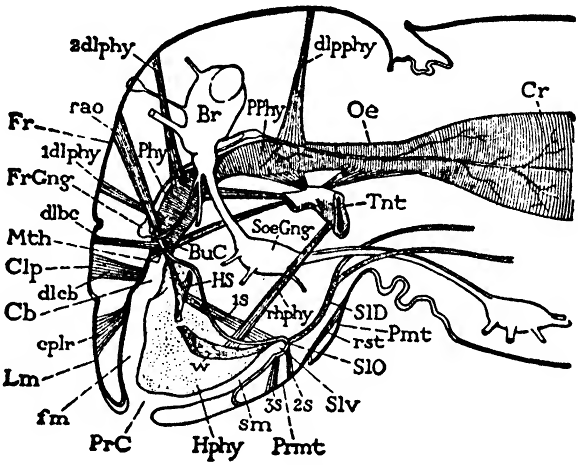


FIG. 131. Sectional diagram of the head of a chewing insect showing the generalized stomodeal and hypopharyngeal musculature. *Br,* brain; *BuC,* buccal cavity; *Cb,* cibarium; *Clp,* clypeus; *Cr,* crop; *Fr,* frons; *FrGng,* frontal ganglion; *Hphy,* hypopharynx; *HS,* hypopharyngeal suspensorium; *Lm,* labrum; *Mth,* mouth; *Oe,* oesophagus; *Phy,* pharynx; *Pmt,* postmentum; *PPhy,* posteriorpharynx; *PrC,* preoral (mouth) cavity; *Prmt,* prementum; *SlD,* salivary duct; *SlO,* salivary orifice; *Slv,* salivarium; *SoeGng,* suboesophageal ganglion; *Tnt,* tentorium; *fm,* food meatus; *sm,* salivary meatus; *w,* basal sclerite of hypopharynx. Other small letters indicate muscles. Note especially the food meatus (*fm*), cibarium (*Cb*), and the salivary meatus (*sm*), important in ingestion. (After Snodgrass)

beetles, which lack salivary glands, eject their intestinal enzymes through the mouth onto their prey. When digestion has occurred, the fluids produced are reabsorbed. Flesh-feeding maggots extrude proteolytic enzymes from the anus and effect extraintestinal digestion of the tissues in which they live and which form their food.

Ingestion. Insects take their food into the alimentary canal by way of the mouth. In insects with chewing mouthparts, the mandibles and maxillae cut off and shred the food. The closing together of these opposing structures presses the food to the back of the mouth at the base of the hypopharynx, fig. 131. The hypopharynx is then pulled upward and forward, forcing the food into the pharynx, which is the anterior end of the oesophagus. From this point the food is moved along the digestive tract by peristaltic action. In insects with sucking mouthparts, fig. 132, the pharynx forms a bulblike pump, which expands and contracts by action of head muscles. The *pharyngeal pump,* as it is called, pulls the liquid food through the beak and into the region of peristaltic control. Digestive enzymes or other secretions may be mixed with the food before it is swallowed.

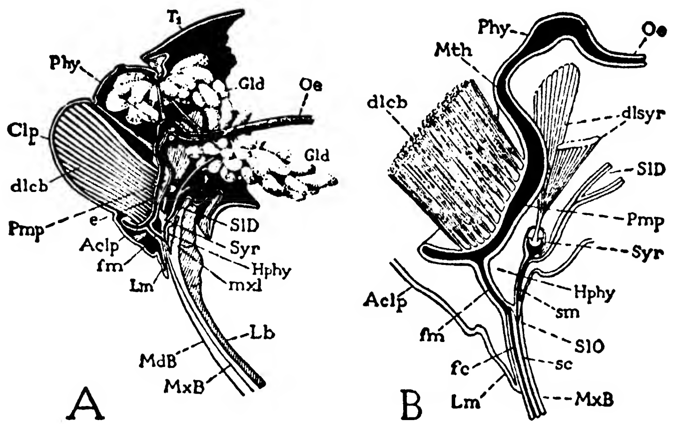


FIG. 132. The sucking pump and salivary syringe of a cicada. *A,* section of the head showing position of the sucking pump (cibarium) with dilator muscles arising on the clypeus. *B,* section through the mouth region, showing food meatus (*fm*), suck pump (*Pmp*), and salivary syringe (*Syr*). *Aclp,* anteclypeus; *e,* true mouth cavity or cibarium; *fc,* food channel; *fm,* functional but secondary mouth; *Gld,* salivary glands; *Lb,* labium; *MdB, MxB,* mandibular and maxillary bristles; *mxl,* maxillary plates; *sc,* salivary channel; other abbreviations as in fig. 131. (After Snodgrass)

The only known exception to oral ingestion occurs in the earliest larval stages of some internal parasites which absorb their nutriment through the general body surface from the tissues or blood of their host.

Stomodeum, or Fore-Intestine. The food is passed through the oesophagus into the stomodeum. There is considerable variety in the functions of the stomodeum; it may serve simply as a passage into the mesenteron, or may be enlarged to form a capacious crop in which the food can be stored and partial digestion may take place. In some cases, as the Orthoptera, digestive juices are passed from the mesenteron to the stomodeum to aid in this.

The stomodeum typically consists of a layer of simple epithelial cells, fig. 134*A*, which secrete a definite cuticle. It is believed that this cuticle is practically impermeable to both enzymes and to the product of digestion and that little or no absorption takes place through it. The function of the cuticle is probably to prevent absorption of only partially digested compounds, because such premature absorption would interfere with complete digestion.

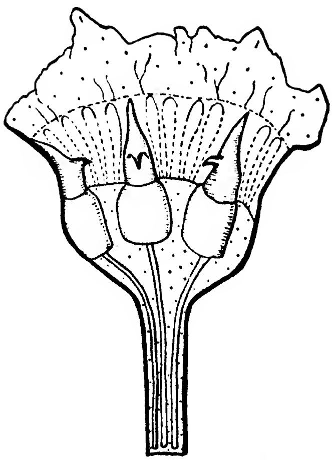


Fig. 133. Proventriculus of a cockroach laid open to show three of the six macerating teeth.

Proventriculus. Orthoptera and other groups which eat coarse food have a set of powerful shredding teeth in the proventriculus for dividing the food into smaller particles. A typical arrangement is that found in the cockroach, fig. 133, wherein six stout teeth do the shredding. Fleas employ a mass of sharp, needle-like teeth directed backward. During digestion these are driven backward at the same time that the blood meal in the mesenteron is thrust forward, and the fine teeth pierce the blood corpuscles, causing them to disintegrate. These movements are caused by rhythmic and opposing muscle contractions. In other insects the proventriculus is simply the narrowed end of the stomodeum.

Mesenteron or Mid-Intestine. In this portion of the alimentary canal the epithelial cells, fig. 134*B*, are exposed, since they do not secrete a cuticle. Certain of these exposed cells perform most of the actual food absorption, and other cells carry on enzyme secretion.

The actual secretion of enzymes by the epithelial cells is accomplished by two methods: (1) *holocrine secretion,* in which the cells disintegrate in the process, emptying their contents into the lumen of the intestine; and (2) *merocrine secretion,* in which the enzymes diffuse through the cell membrane into the lumen. The former is illustrated in fig. 134*B*. This shows the clusters of regenerative cells, or nidi, which replace the cells used up during holocrine secretion.

Enzymes. If the salivary glands produce the starch enzyme *amylase,* the mesenteron may produce chiefly sugar enzymes such as *maltase,* the fat enzyme *lipase,* and the protein or proteolytic enzymes *pepsin* and *trypsin*. Production of enzymes is also correlated with diet. Omnivorous insects such as the cockroach produce the full complement of enzymes for digesting all types of food. Blood-sucking insects, however, produce chiefly proteolytic enzymes. Some insects secrete cellulase for digesting cellulose. The wax moths digest wax, and the clothes moths digest keratin, but the enzymes which enable them to do this have not been isolated.

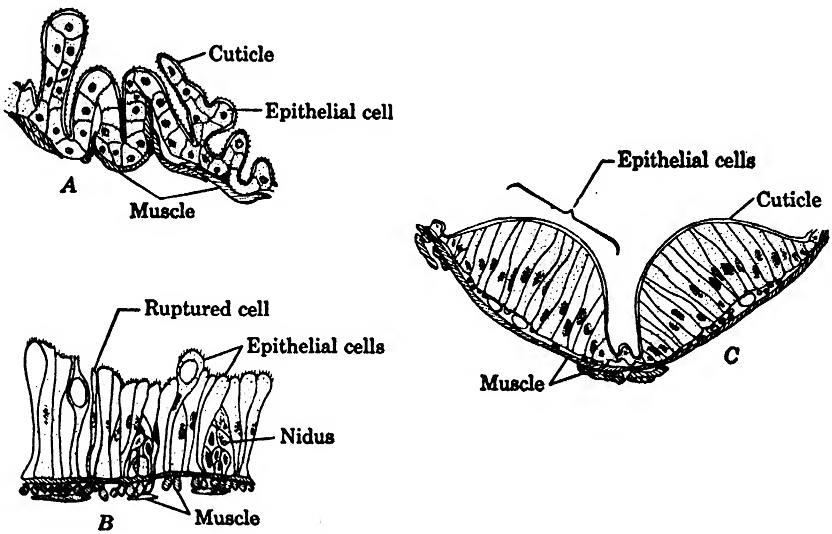


FIG. 134. Cell structure of portions of the digestive tract of a cockroach. *A*, stomodeum, longitudinal section; *B*, mesenteron, longitudinal section; *C*, proctodeum, cross section.

Peritrophic Membrane. The epithelial cells of the mesenteron are exposed and delicate. If the food bolus were to be pushed over the unprotected surface of these cells, it would undoubtedly injure them severely and interfere with their functions of secretion and absorption. In vertebrates, mucous glands coat and lubricate the food boluses and hard particles to avoid abrasive injury to stomach epithelium. Insects have no mucous glands but obtain protection for the epithelium by the formation of a *peritrophic membrane*, fig. 135. This membrane forms a continuous tubular covering around the food mass. The membrane is composed of chitin; it is freely permeable to both digestive enzymes and all the products of digestion. Its remarkable permeability has been demonstrated experimentally by the use of dyes.

The formation of the peritrophic membrane is a topic of considerable interest. In a great many insects, it originates from a secretion of the general surface of the mesenteron. This chitinous secretion is formed into a layer over the parent epithelial cells and then separated from them to form a sort of tube around the food mass. The tube usually remains attached at the anterior of the mid-intestine where the fore-intestine projects into it.

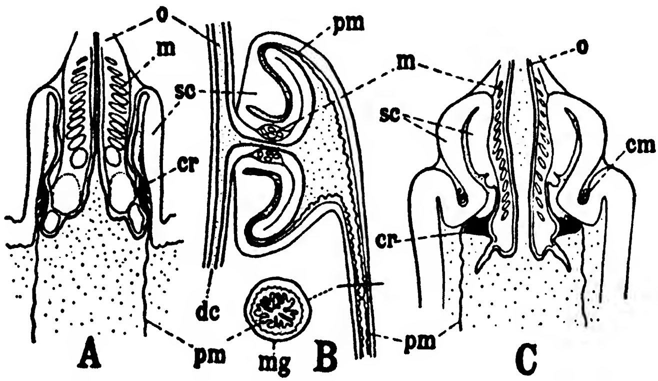


FIG. 135. Annular molds producing a peritrophic membrane. *A,* larva of mosquito, *Anopheles; B,* tsetse fly, *Glossina; C,* earwig, *Forficula. cr,* cuticular ring forming inner wall of press; *cm,* circular muscle compressing outer wall against this ring; *dc,* duct of crop; *m,* sphincter muscle; *mg,* mesenteron in cross section; *o,* oesophagus; *pm,* peritrophic membrane; *sc,* cells secreting the substance of the membrane. (After Wigglesworth, "Principles of Insect Physiology," by permission of E. P. Dutton and Co.)

The peritrophic membrane is not formed in certain insect groups which take only liquid food, including Hemiptera, Anoplura, and adults of fleas, mosquitoes, and horseflies. It is absent also in a few other groups, notably the Carabidae, Dytiscidae, and Formicidae.

Cardia. In some groups of insects the peritrophic membrane is secreted by a specialized group of cells around the anterior end of the mesenteron. The secretion is pressed or molded into a membrane by the outward pressure of either the mesenteron entrance as it is distended by incoming food, or by a special organ called a *cardia.* This structure is most highly developed in the Diptera and Dermaptera, fig. 135. It consists principally of a sclerotized ring around the opening into the mesenteron, which presses against the walls of the intestine a flow of secretion from the group of cells just anterior to it. As the membrane is formed, it is passed back through the intestine as a sheath around the food.

Proctodeum or Hind Intestine. The function of this part of the digestive tract is still not well understood in many insects, although it is thought that normally no absorption of food occurs here. The epithelial cells secrete a definite cuticle, fig. 134*C*, as in the stomodeum, but this cuticle is readily permeable to water. The posterior part, forming the rectum, is usually heavily muscled to compress the residue of the food after digestion and so form the excrement into pellets before defecation. Two other functions are well established:

1. Water Absorption. All insects which must conserve water to the utmost rely on the proctodeum to absorb water from the excrement and return it to the body. In such insects as the mealworms, the epithelial cells in the rectum may extract almost all the water from the excrement, leaving it a dry pellet. The water absorption plays an especially important role in excretion, under which it is discussed more fully.

2. Symbiotic Digestion. Termites, certain wood cockroaches, and certain scarab-beetle larvae, whose chief diet is wood fiber, have no enzyme for digesting the cellulose they eat. They rely instead on a rich symbiotic fauna of microorganisms in the intestine, which digests the cellulose and makes it available to their host. This fauna is usually contained in the proctodeum, and there the cellulose digestion occurs. Whether or not the digested material is returned to the mesenteron for absorption is not known. Investigations of symbionts in other insects have brought out many apparent contradictions and questions, showing the need for more research in this field.

Adaptations to Liquid Diet. Various insects which suck blood or plant juices have evolved methods for extracting much of the water from the food before it comes into contact with the digestive enzymes. This arrangement has two advantages: (1) Some of the assimilable sugars in the food may be absorbed rapidly, and (2) the enzymes do not suffer undue dilution. The partial dehydration is accomplished by the following methods.

1. In adults of many Diptera the mesenteron is divided into several sections, each with a different type of epithelium. It is thought that the first section acts as an absorption area to take out much of the water from imbibed liquids.

2. In such blood-sucking Hemiptera as the bedbugs the first part of the mesenteron forms a large crop in which the blood meal is received. This "crop" absorbs much of the water and so concentrates the blood before it is passed to the region in which the enzymes are produced.

Note that in the Diptera and the bedbug the water is absorbed from the mesenteron and passed into the insect's blood stream. From the blood stream it is excreted through the Malpighian tubules into the proctodeum.

3. The scale insects, cicadas, and most other Homoptera feed entirely on plant juices. In order to get ample nourishment a relatively tre-

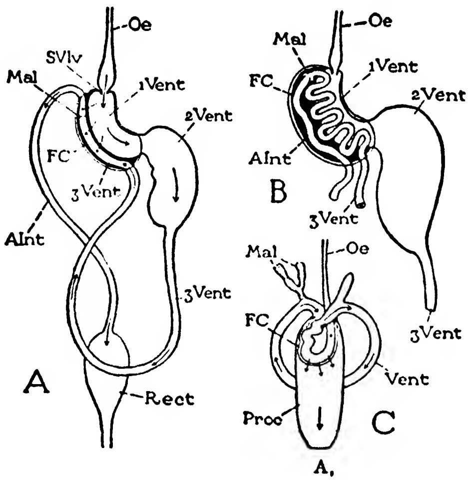


FIG. 136. The filter chamber of Homoptera. *A*, diagram of a simple type of filter chamber in which the two extremities of the ventriculus and the anterior end of the intestine are bound together in a common sheath. *B*, the ventriculus convoluted in the filter chamber and the intestine issuing from its posterior end. *C*, the filter chamber of the scale insect *Lecanium*, diagrammatic. *AInt*, proctodeal intestine; *FC*, filter chamber; *Mal*, Malpighian tubules; *Oe*, oesophagus; *Proc*, proctodeum; *Rect*, rectum; *SVlv*, stomodeal valve; *Vent*, a section of the mesenteron. (From Snodgrass, after Weber)

mendous volume of plant juice must be taken in by an individual, with a proportionately large volume of water. This excess water is disposed of by an ingenious structure called the *filter chamber*. The principle underlying this chamber is very simple. The anterior part of the mesenteron lies beside a part of the proctodeum, and so intimate are the two that much water from the incoming juices in the mesenteron is passed directly through the two adjacent intestinal walls. Presumably the direction of water passage is controlled by the permeability of the epithelial membranes. This concentrates the juices, which then pass normally through the full course of the mesenteron and are digested. The excess water thus short-circuited into the proctodeum is exuded from the rectum as honeydew.

Many designs of filter chambers occur. Either the adjacent parts of the mesenteron and proctodeum are bound together by an enveloping sheath, or the mesenteron may be embedded into a cavity or fold of the proctodeum. The operation of all of them follows the general plan in fig. 136, which is semidiagrammatic.

Larval Adaptations. A peculiar modification of the digestive tract is found in the larvae of the higher Hymenoptera and Neuroptera. The end of the mesenteron is closed and does not connect with the proctodeum. The mesenteron, during larval development, becomes greatly distended with fecal matter. Prior to pupation the two sections of intestine become joined, and the fecal pellet for the *entire larval life* is evacuated.

Stomach Reaction. The contents of the digestive tract in most insects average slightly acid, with a *p*H of 6–7. The saliva is usually neutral. In plant-feeding insects the intestine averages more alkaline and has been recorded as high as *p*H 8.4 to 10.3 in the silkworm larva. Carnivorous or flesh-feeding insects usually average on the more acid side. Acidity of *p*H 4.8 to 5.2 has been observed in the crop of the cockroach after a carbohydrate meal; it has been suggested that this acidity is the result of fermentation by microorganisms, but it might be due to acid secretion of certain cells of the salivary glands. The greatest acidity recorded is *p*H 3.0 in a portion of blow fly larvae intestine.

Cardiac or Gastric Caeca. Little is known about the function of these processes. It has been suggested that they house the regenerative supply of the normal bacterial fauna of the intestine.

ASSIMILATION AND NUTRITION

Assimilation. Because many insects ingest mixtures of carbohydrates, fats, and proteins, and produce conventional enzymes for their digestion, it is to be assumed that, in general, their assimilation follows the same pattern as vertebrates'. The actual proof of this is negligible, and it is possible that reactions and processes take place which are at present unknown. Other unknowns include the manner and place in which carbohydrates are converted to fats, where deamination of proteins occurs, and other intermediate stages of assimilation.

Nutrition. Insects such as the cockroach seem to require about the same variety of food as humans, but food requirements of many insects are not what they seem. Insects which feed only on sugars in the adult stage usually feed on a different or varied diet in the larval stages. Other insects may have symbiotic organisms in their digestive tracts which convert a food such as cellulose into a variety of compounds. Still other insects may appear to eat wood or other inert matter, but actually feed on fungi, diatoms, or other microorganisms growing on the inert matter. Although our knowledge in this field is far from complete, it is obvious that insects as a whole eat almost every conceivable substance and, with or without the help of symbionts, extract the essential supply of proteins and combustibles.

Vitamins. Investigations to date indicate that insects probably need the A and B complex vitamins, but not vitamin C. Some, however, appear to need factors not yet discovered in vertebrate nutrition. It has been shown with experiments on blow fly larvae that some of these vitamins can be obtained from symbionts or from microorganisms mixed with the normal diet.

Water Requirements. As in other organisms water is a fundamental basis of metabolic processes since practically all of them occur in aqueous solution. Hence water is a very important item of the insect diet. Insects have developed many structural and physiological specializations to conserve water. Most of them obtain an abundance for their needs in foodstuffs with a fairly high water content, such as foliage and blood. There are cases in which water is conserved to such a high degree that the insect is able to exist entirely on dry materials. In these instances the insect makes use of the water resulting from the oxidation of the foodstuffs. But even in most of these cases the food must contain a small percentage of water to supplement the metabolic water. An unusual property is found in the mealworm: In atmospheres of high humidity it can actually absorb water from the air.

EXCRETION

Many waste products of metabolism either are of no value to the organism or would be harmful if allowed to accumulate. The process of eliminating these waste products is excretion. The elimination of carbon dioxide and some water is technically excretion but for convenience is treated under respiration. Excretion, as treated here, is restricted to the elimination of excess water, salts, nitrogenous wastes such as uric acid, and various undesirable organic compounds.

In insects the Malpighian tubules are the chief known organs of excretion. In addition, certain excretions may be deposited in the cuticle or setae as pigments. The use of the dye indocarmine as an indicator has demonstrated also that in the Thysanura part of the salivary glands may be excretory in function.

Several tissues, such as the fat bodies and molting glands, have been considered as excretory in function because of the deposition of uric acid crystals within their cells. Uric acid, however, is the end product of protein metabolism and precipitates out as crystals very readily. It is believed that the observed uric acid crystals in many tissues are due simply to rapid protein metabolism, resulting in the production of uric acid too fast to be entirely taken up by the blood. Under these conditions the excess uric acid is precipitated as crystals in the cells in which it is formed, to be dissolved and eliminated at a later time.

Malpighian Tubules. These organs excrete chiefly uric acid. In most insects the excretion is accomplished by circulation of water, as is the case in most of the vertebrates.

In its simplest form in insects this process is as follows: The uric acid (probably in the form of a sodium or potassium salt) in the body cells is diffused into the blood, which eventually circulates around the Malpighian tubules. All or part of the cells of these tubules absorb the uric acid from the blood and discharge it, in aqueous solution, into the lumen of the tubule. From this point uric acid solution, or urine, is forced into the proctodeum and voided through the anus.

This method of excretion requires a continuous supply of water, and with very many insects water is at a high premium. Very likely the basic solvents (sodium and potassium salts) are equally valuable. In order to conserve them, various methods have been evolved to extract the water and base from the urine and return them to the blood or to the upper end of the tubules.

One method, exemplified by earwigs and grasshoppers, is the development of absorptive areas in the rectum, fig. 137. These areas extract the water from the excrement and return it to the blood. In forms such as the mealworm, fig. 138, the tips of the Malpighian tubules are bound to the rectum by a membrane. Apparently here the absorptive powers of the tubules are added to those of the rectum, for in these forms the excrement is dried to a powder. It is also probable that the absorbed water is returned directly into the tubules, and thus the same water is reabsorbed and used over and over again.

A second modification is that in which the cells of the lower part of the Malpighian tubules extract water and base from the urine. In these cases the upper part of the tubules contains a clear liquid, and the lower part contains solid crystals of precipitated uric acid. These are pushed into the proctodeum for evacuation. The cells of the two areas have well-marked histological differences. It may be that here also some of the water is used continuously, much as arrows in

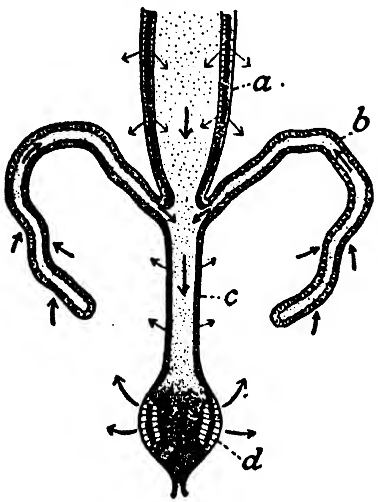


Fig. 137

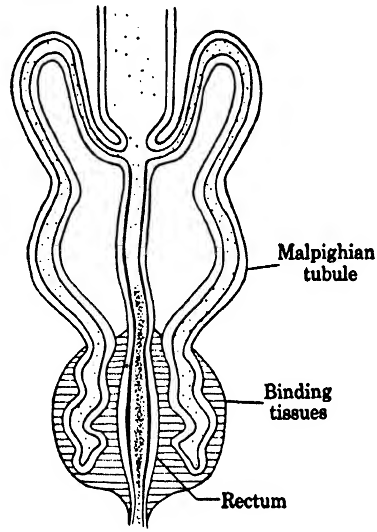


Fig. 138

Fig. 137. Diagram of water circulation in alimentary and excretory systems of an insect. Arrows indicate direction of water movement. *a*, mesenteron; *b*, Malpighian tubes; *c*, proctodeum; *d*, rectal glands. (From Wigglesworth, "Principles of Insect Physiology," by permission of E. P. Dutton and Co.)

Fig. 138. Relation of Malpighian tubules and rectum in mealworm *Tenebrio*. (Adapted from Wigglesworth)

fig. 137 indicate. Many insects, such as the larvae of Lepidoptera, combine all these methods.

In the Malpighian tubules of many insects, deposits of carbonates have been found. It is not known why these are present or what becomes of them. Their presence suggests that the Malpighian tubules may have other excretory functions, in addition to those relating to uric acid and water.

Pigments. Certain wastes of metabolism may be converted into pigments (some of them derivatives of uric acid), and these are often deposited in the cuticle. In the butterfly family Pieridae these pigments are deposited in the scales of the wings, in the Colorado potato beetle they are deposited in the sclerites; in both they form the color pattern of the insect. The conversion of metabolic wastes into pigments is likely a common phenomenon among insects.

Glandular Secretions. Certain glands which secrete wax, scents, and other substances may be able to utilize waste products as a basis for their secretions. There is little experimental evidence to support this conjecture.

METABOLISM

Metabolism is the total of all the chemical and physical processes which take place within the organism. This includes both the constructive phase (anabolism) and the destructive phase (catabolism). The metabolism of insects is affected markedly by both the activities of the insect itself and the external conditions which surround it, such as temperature, humidity, and atmosphere. These influences on fundamental metabolism integrate with those on actions and habits, as discussed under Ecological Considerations, in Chapter 9.

Temperature Control. Insects are cold-blooded animals in that their body temperature, in general, depends on that of the environment. Within certain limits, insects can change their body temperature. At high temperatures insects of sufficient size can reduce their temperature by evaporation of water from the surface. At low temperatures the chemical changes going on within the body may raise its temperature above that of the environment. Certain soil-inhabiting beetles, for example, have been observed to depress the body temperature 3.6°F.(= 2°C.) by tracheal evaporation. Evidence indicates that fairly high body temperatures are necessary for the extremely rapid muscular activity of flight. For instance, experiments with large hawk moths have demonstrated that they cannot fly at body temperatures below 86°F.(= 30°C.). Below this point the moth stands and vibrates its wings until this muscular activity has raised its temperature to 86°F., at which point it can fly. During flight its temperature may rise above 104°F. (= 40°C.), owing to the violent muscular action.

To what extent insects at rest increase their metabolism to maintain body temperature is not known.

Metabolic Rate. Within certain limits the metabolism of an insect increases with an increase in temperature. This variation in metabolic rate is correlated with the following physicochemical phenomena which automatically accompany a rise in temperature:

1. Chemical reactions increase in rate.
2. Solubility of solids in liquids increases.
3. Speed of diffusion of gases increases.
4. Solubility of gases in liquids decreases.

In insects an increase in temperature also induces an increase in activity, which in turn increases metabolism. Humidity also influences metabolism; it has been demonstrated in several insects that an increase in humidity decreases the rate of metabolism. These correlations obviously do not operate below or above temperatures detrimental to the insect's well-being or under inimical combinations of temperature and humidity.

Various attempts have been made to show definite mathematical relationships among temperature, humidity, basal metabolism, activity, and growth. So many variables have been encountered that few workers agree regarding the interpretation of results.

The resting metabolism of the bee is proportionate per unit of weight to that of man, consuming about 20 gram-calories of heat per kilogram of weight per minute. But in extremes of exercise the bee may increase this as much as 1300 times, whereas man in his greatest exertions is able to increase it only 10 or 12 times. Thus the bee in flight consumes as high as 26,000 gram-calories (= 26 standard or large calories) per kilogram of weight per minute.

In insects which are normally well fed, the respiratory quotient during activity is near unity, indicating that only carbohydrates are being oxidized. During starvation the quotient falls, a phenomenon associated with the oxidation of fats and proteins. This indicates that, under starvation conditions, insects follow the same procedure as other animals, burning their carbohydrates until these are exhausted, and only then using the fats and proteins for energy.

Oxygen Requirements. Insects are remarkably resistant to oxygen deficiency. The rate at which they are able to extract oxygen from the atmosphere remains the same down to a very low level of oxygen pressure. The exact level differs in various species. Below the critical oxygen pressure, the rate at which it is absorbed drops rapidly.

Certain insects possess a peculiar *anaerobic tolerance;* they are able to exist for long periods in the complete absence of oxygen. In these circumstances, the insect stops its activities and become quiescent. Only a minimum of metabolism goes on, and it probably consists chiefly of the involuntary muscular activities controlling circulation and digestion. The lactic acid, other unoxidized metabolites, and carbon dioxide from these processes accumulate in the body. When air is again available, the insect absorbs oxygen from it at an extremely high rate, in order to oxidize the waste products accumulated during the anaerobic period. This anaerobic tolerance has been demonstrated experimentally in many insects. The larva of the horse bot *Gasterophilus* (parasitic in the stomach of the horse) normally enjoys a cycle of aerobic and anaerobic conditions correlated with digestive activities of its host. Experimentally it has been found that the bot larva can survive as long as 17 days without oxygen. Diurnal aerobic and anaerobic cycles undoubtedly occur in certain lake-inhabiting insects which may hide below the lake's thermocline during the day and feed near the oxygen-carrying surface layer of water at night.

Temperature Resistance. In the course of their lives insects may be exposed to great extremes of temperature. Insects that have lost water by desiccation are more resistant than normal ones to inimical temperatures. The exact reason for this is not known. It has been shown that desiccated individuals of the beetle genus *Leptinotarsa* may withstand 1° to 8° of temperature (F.) above the point which is lethal to undesiccated individuals. Similarly desiccated individuals are more resistant to cold.

There is as yet no complete explanation of these phenomena related to partial desiccation. The cold resistance is thought to be due in part to a lowering of the freezing point of the cell contents by simple concentration of dissolved substances. Another reason given is that more of the free body water goes into combination, or is "bound," with body colloids. It is thought that such a depletion of free water by its conversion to bound water lowers the freezing point of the body contents and thus effects a greater degree of cold hardiness. But the exact chemical and physical changes, and their significance, are not known. The explanation of increased resistance to heat probably hinges on similar changes.

Color-Pigment Metabolism. The color pigments of insects (see p. 122) show interesting reactions to both metabolism and external conditions. Experiments on many insects, including the potato beetle *Leptinotarsa* and its predator, the stink bug *Perillus,* have shown that, as the metabolism increases with higher temperature or lower humidity, more of the pigments are oxidized, resulting in lighter-colored insects. Both the black melanin and the orange carotinoids have been found to react in this fashion in some insects. In these cases (for example, the Colorado potato beetle), individuals reared at a high temperature and low humidity may be almost colorless; others raised at medium temperatures and humidity may be orange; and still others raised at low temperatures and high humidity may be black.

The application of these effects is restricted. In certain insects only some parts of the body show these reactions. In others the color pattern may be rigidly fixed and apparently not influenced by effects of external conditions.

The most spectacular cases of color changes are those in which the insect adapts its color to that of its surroundings. The walkingstick *Dixippus* is pale by day and dark at night; the color change is accomplished by a clumping or spreading of the pigment granules in each epidermal cell. This change is brought about by many stimuli acting through the eyes or tracheal system on a nerve center in the brain; this apparently causes the secretion of a hormone which circulates in the blood and determines pigment movements in the cells. The larvae and pupae of certain Lepidoptera possess the power of acquiring the tone or coloration of their background. Careful observations seem to show that in the *Pieris* pupa the quality of light reflected from its surroundings and passed through the eyes of the pupating larva is the original stimulus for pupal color. This light stimulus apparently acts through a nerve center which liberates hormones, causing color deposition in the pupal epidermis.

Development Control and Metamorphosis. Considerable evidence is accumulating which indicates that in insects development is influenced by internal factors other than nutritional requirements. Experiments by Wigglesworth and others on the development of decapitated insects have brought forward interesting ideas. They suggest very strongly that a hormone-like substance is produced in the head which retards sexual development, without interfering with increase in size. Carrying this idea further, Wigglesworth points out that such a hormone could explain the complex phenomenon of complete metamorphosis, in which the early stages grow chiefly in size and practically all adult characters are developed in the pupal stage.

Metamorphosis. In insects with incomplete metamorphosis the physical changes leading to adulthood are spread more or less evenly throughout the entire life. In insects with complete metamorphosis the assumption of adult characters is accomplished suddenly, in the pupal stage. There is at this period an apparent physical revolution from the larval to adult characteristics. There is, however, no accompanying all-inclusive physiological revolution. The epidermis and tracheal system are reconstructed simply by the normal secretion of their matrix cells, but the secretions are cast in a different "mold." The nervous system enlarges rapidly by growth of the constituent parts, sometimes accompanied by the fusion of certain ganglia. The heart grows without marked change. The digestive tract is changed by the growth or reduction of some parts and the remodeling of others.

Not represented in larval structures are certain features of adults, such as the wings and reproductive system. Certain other adult features are usually radically different in size or organization from their larval counterparts, notably the legs and the musculature (especially muscles controlling flight and reproductive activities). These adult parts are built up from larval fat bodies, blood sugar, and muscles, in a series of conversion processes which are grouped into two phases, *histolysis* and *histogenesis*. Histolysis is a breaking-down process, essentially catabolism; leucocytes and enzymes convert the larval fat body, most of the muscle tissue, undoubtedly parts of other tissue also, and later the leucocytes themselves, into a nutritive matrix transportable by the blood to growing tissues. Histogenesis, representing anabolism, is the construction of adult tissues from the products of histolysis. Both phases go on simultaneously.

Before pupation, larvae enter a quiescent stage lasting one to several days. It is during this period that the conversion processes begin. They continue through the pupal stage until the adult structure is complete. During these processes, the stores of fat and glycogen accumulated by the larva during its feeding period are almost entirely depleted.

Suspended Activity: Diapause. In the life of many insects there are more or less prolonged periods of rest or quiescence, during which visible activity and many physiological processes are suspended. These periods are called diapause and may occur in the egg, nymph, larva, pupa, or adult. They are characterized chiefly by a cessation of growth in immature stages and by a cessation of sexual maturation in adults.

Diapause is brought about by various adverse conditions, heat, drought, cold, and so on. It is exemplified by the estivation period in which caterpillars pass the hot dry summer period, and by the hibernation period in which various stages pass the winter. The duration of diapause varies with the species and presents some interesting considerations. In some species diapause lasts only until the unfavorable conditions end; then the insect immediately resumes its normal activities. In others the return of favorable conditions alone does not break diapause, but some other stimulus, such as cold, parasite oviposition, or food conditions, activates the break. This point is well illustrated by the reaction of certain mosquito eggs. The eggs of *Aedes vexans* are laid on damp soil and undergo diapause or suspended development until the egg bed is flooded to form a pool suitable for the larvae. *Aedes canadensis* eggs may be laid in the same situation as those of *A. vexans*, but they will not hatch, even with flooding, until they have been subjected to cold. Eggs of both species are frequently laid together in early summer; those of *A. vexans* hatch in the pools formed by late summer rains, but those of *A. canadensis* carry over the winter and hatch in the spring rain pools.

A third factor, time, enters the picture in still other insect species. In these not only are various stimuli required to break diapause, but also a certain length of time must elapse before the stimuli cause the break. This time factor has been demonstrated in studies of the hibernation characteristics of certain cutworms.

Many surmises have been made regarding the reason for initiation and breaking of diapause. It has been suggested that, since growth appears to be the chief activity affected, the actual regulation of diapause is accomplished through regulation of the growth hormones. Our knowledge of this whole question is in only its groping stages. Diapause and hormone research is one of the most inviting fields in fundamental entomological research.

RESPIRATION

Supplying oxygen to the tissues and disposing of the carbon dioxide is the process of respiration. It is accomplished in most insects by the tracheal system. This is in essence a system of open tubes, and through these the air is brought directly to the tissue cells.

Tracheae and Tracheoles. The tracheae are invaginations of the ectoderm, and their general character is similar to that of the epidermis, fig. 139. The foundation structure is a layer of flat epithelial cells; these secrete the lining of the tracheae, a cuticle-like substance, called the *intima*. The surface of the intima is thickened by spiral filaments or *taenidia;* these spiral taenidia give the trachea great strength to resist pressure and insure that the trachea remains round and open even under conditions of bending and pressure. The tracheae divide and redivide, becoming smaller and smaller; finally each ends in a cluster of minute branches, the *tracheoles*. Unlike the tracheae, the tracheoles have no regular layer of epithelial cells, but are minute simple cuticular tubes; these possess taenidia, to date demonstrated only by the electron microscope. The base of each cluster of tracheoles has a weblike cell, the tracheole cell, with extremely thin protoplasmic

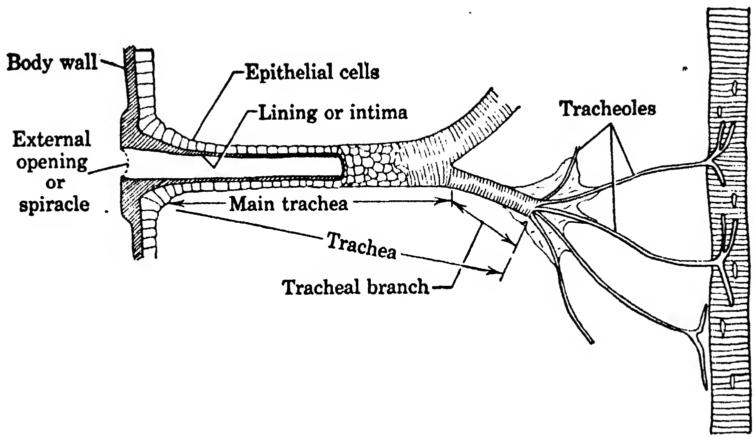


FIG. 139. Diagram of an open trachea of an insect.

extensions. These extensions appear to surround and follow the tracheoles. The tips of the tracheoles lie alongside, between or actually within the tissue cells of the body. It is believed that through these tracheole tips occurs most of the respiratory gas exchange of the tissues.

The properties of the tracheae and tracheoles are quite different from those of the epidermis. Both tracheae and tracheoles are permeable to gases, presumably extremely so where the wall is as delicate as in a tracheole. The tracheae are impermeable to liquids; the spiracles at least are extremely hydrophobic, that is, the surface resists the entry of water. The tracheoles, especially their tips, are readily permeable to liquids.

Tracheole Liquor. In many insects the tips of the tracheoles contain a certain amount of liquid of unknown composition. When associated with relaxed muscle, fig. 140*A*, this liquor may rise a considerable distance in the tracheoles; when the muscle is fatigued, a large part of the liquor is withdrawn from the tracheole into the cells, fig. 140*B*. It is possible that this retraction is due to the increased osmotic pressure of the muscles resulting from acid metabolites incurred during contraction. Such an action on the liquor has the effect of drawing the air into intimate contact with the fatigued cell and presumably aids in increasing the oxygen supply to working tissue in which the oxygen need is greatest.

Diffusion. The actual mechanics by which oxygen is conveyed from the spiracles, through the length of the tracheae and tracheoles, and finally to the tissues, and by which carbon dioxide is eliminated along the reverse path, has been the subject of many theories. It is now

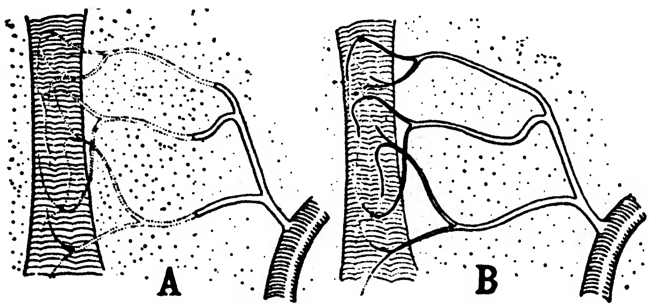


FIG. 140. Rise and fall of liquor in tracheoles. *A*, high level in rested state; *B*, low level in fatigued state. Tracheoles shown with dotted lines contain liquid, those with plain lines contain air. (From Wigglesworth, "Principles of Insect Physiology," by permission of E. P. Dutton and Co.)

generally accepted that these gases are conveyed by diffusion, with the help of some mechanical ventilating in certain insects. Recent analyses have been made of dimensions of tracheae, oxygen consumption, and the diffusion coefficient of oxygen of various insects. They have shown that, even in the case of large caterpillars, diffusion alone will provide a sufficient stream of oxygen to the tracheole endings if the oxygen pressure in them is only 2 or 3 per cent below that of the atmosphere.

This same reasoning accounts also for the elimination of carbon dioxide, since it has a rate of diffusion only slightly less than that of oxygen. Analysis of carbon dioxide elimination, however, has shown that nearly a fourth of the amount produced in the body is eliminated over the general body surface. This is explained by the fact that carbon dioxide diffuses *through animal tissues* about 35 times as fast as oxygen. Consequently, any carbon dioxide formed in metabolism diffuses not only into the tracheoles but also into surrounding tissues in all directions and eventually to the exterior through the body wall.

Blood Respiration. Normally the blood plays no important part in transporting oxygen from the atmosphere to the tissues. But it should be borne in mind that the blood itself is an extensive living tissue which requires oxygen for its maintenance and functioning and carbon dioxide disposal to remain healthy. Because the blood passes over and among many trachea and tracheoles, it has a ready supply of oxygen throughout its course in the body cavity. Any excess carbon dioxide in the blood will ultimately escape through either the tracheal or body wall.

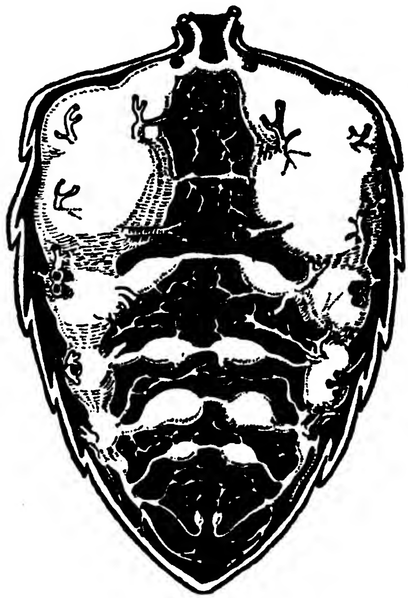


Fig. 141. Tracheal system in the abdomen of the honeybee worker, showing the air sacs. Dorsal tracheae and air sacs have been removed. (From Wigglesworth, after Snodgrass, "Principles of Insect Physiology," by permission of E. P. Dutton and Co.)

Ventilation of the Tracheal System. For many small or sluggish insects, gaseous diffusion alone is sufficient to satisfy the needs of respiration, but it is not adequate for active running and flying forms with a high metabolic rate and large energy consumption. These forms have supplemented diffusion with mechanical ventilation of the tracheal system. Two principal types of structures are used for this purpose.

1. The taenidia of the trachea prevent their being flattened but in some instances allow a longitudinal contraction and expansion like an accordion. The contraction may result in a reduction of capacity of as much as 30 per cent of the expanded volume.

2. Certain portions of the tracheae may be elliptic instead of round and have weak taenidia or none at all. These elliptic portions form sacs which can be flattened by an increase in blood pressure or by bending. In many instances these air sacs form distinct enlarged chambers, resembling the elliptic tracheal structures in having no taenidia and being readily compressible, fig. 141. The action of these is like that of a bellows.

Both these structures act as air sacs analogous to lungs. The respiratory movements of the insect body cause alternate filling and emptying of these sacs. When the body is contracted, the accordion-like sections are contracted, or the blood pressure is increased and results in a compression of the air sacs. Both actions cause an ejection of air from the sacs through the spiracles. When the body is relaxed, the air chambers expand, owing to their own elasticity, and fill up with air from the outside.

The effect of this ventilation, fig. 142, is to keep the air sacs and tracheal trunks filled with air similar in composition to that of the

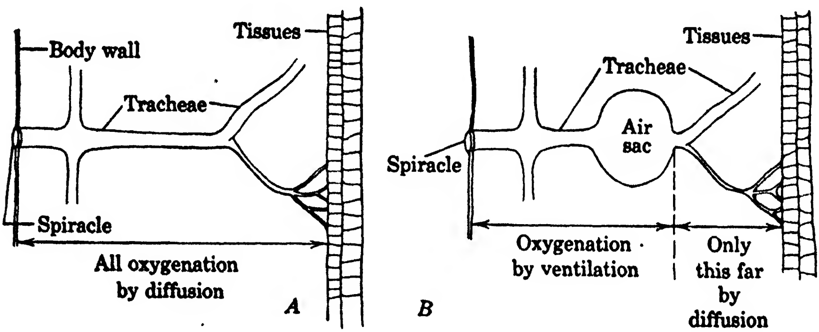


Fig. 142. Diagram to illustrate relation between diffusion and ventilation. *A*, system without ventilation, relying entirely on diffusion; *B*, system supplementing diffusion with ventilation.

atmosphere. Diffusion acts along the remaining short distance to the tissues, through tracheae branching from the sacs or tracheal trunks.

Rhythmic Ventilation. In experimental work it has been observed that frequently there occurs another type of tracheal ventilation, in which air is inhaled through the thoracic spiracles and exhaled through the abdominal spiracles, or vice versa. This draws air through the tracheal trunks. Some investigators consider this an important method of ventilating the system. So little uniformity has been found in the various insect species studied that there is considerable doubt regarding the actual importance of this type of ventilation.

Spiracle Control and Evaporation. Oxygen and carbon dioxide diffuse readily through the tracheal system, and so does water, in the form of water vapor. If the spiracles remain open indefinitely, the insect loses water steadily, and water is normally a precious commodity to the insect. Consequently, to eliminate unnecessary evaporation, the spiracles are kept closed as much as possible, being opened only enough to satisfy the demand for oxygen intake and carbon dioxide discharge.

Respiration Control. Because of the necessity for combining evaporation control with aeration, it is obvious that the opening and closing of the spiracles and the regulation of the respiratory movements must be controlled by some sensitive mechanism. Much work has been done on this phase, many times with apparently contradictory results. From the mass of experimental data there have emerged, nevertheless, a number of interesting generalities, the more important being listed here:

1. The immediate sensory control of respiration is in the segmental ganglia of the ventral nerve cord. Experiments in vivisection have shown that each ganglion may and probably usually does respond individually. Each ganglion controls only its own segment, so that each segment normally acts as an isolated unit as far as respiration is concerned.

2. The brain seems to have little or no effect on respiration. If a modulating or coordinating center exists, which can produce rhythmic action of all or several segments, it is apparently seated in the prothoracic ganglion.

3. During times of rest the respiratory movements may cease altogether, and the spiracles close. In some insects an excess of oxygen will effect the same reaction.

4. Practically any external nervous stimulation (visual, tactile, etc.) will initiate or increase respiratory activities.

5. Various internal chemical stimuli will increase respiration. It is believed that in most species the respiratory nerve center is stimulated by increased acidity of its receptive tissues, caused equally well by either high carbon dioxide tension or acid metabolites produced because of oxygen want. Thus, in cockroaches a high tension of carbon dioxide causes respiratory activity. In mosquito larvae, on the other hand, the carbon dioxide diffuses from the body rapidly and seldom builds up in excess amounts; it is oxygen want that drives these forms to the surface for more air.

Adaptations for Aquatic Life. The foregoing discussion deals with the type of respiration found in terrestrial insects. But many forms either live in water or spend a great deal of time submerged in water.

Several types of adaptations are found to fit the insect for obtaining its respiratory needs in aquatic situations.

1. Diving Air Stores. When they dive beneath the surface, certain insects carry with them a film or bubble of air attached to some part of the body. Both adults and nymphs of water boatmen (Corixidae) and backswimmers (Notonectidae) carry a film of air in the pile on the ventral surface of the body; this film is kept in place by hydrophobe hairs which resist penetration of the air film by the water. Adults of the diving beetles (Hydrophilidae, Dytiscidae) have an air space under the wing covers or elytra, into which space the spiracles open. This air store serves not only as a supply of oxygen for the insect but also as a sort of lung and gill, obtaining added oxygen from the water and discharging carbon dioxide into it by diffusion. It cannot provide for respiratory needs indefinitely in this way, but it enables the insect to remain under water a considerable period before having to come to the surface for more air.

2. Air Tubes. Many insects which live submerged all the time, breathe through a tube or pair of tubes which can break through the surface of the water. Only the pair of spiracles connected with these tubes is functional; the others are either closed or not developed. The mosquito larva, fig. 367, has a rigid tube; when in need of oxygen, the larva swims to the surface and thrusts the end of the tube through the surface-tension membrane and into contact with the air. The rat-tailed maggot, fig. 375, a fly larva which lives in a viscous or liquid medium, does not swim to the surface but has a respiratory tube which can be extended 3 to 4 inches to the surface. Several other kinds of tubes occur in different groups.

3. Cutaneous Respiration. Large numbers of aquatic insect larvae make no contact with the atmosphere and have no external devices or special structures for respiration. In these the gas exchange is made by diffusion through the body wall. The insect utilizes the oxygen dissolved in the water, and excess carbon dioxide diffuses into the water. There are two distinct types of cutaneous respiration. In the first (including very small or first-instar larvae) there is no tracheal system present; in these the gas exchange within the body is by diffusion through the tissues, including the blood. In the second type (including most of the larger gill-less forms such as late-stage midge larvae and many caddisfly larvae) the tracheal system is developed, but instead of spiracles there are clusters of fine tracheae in the epidermis, fig. 143. Here the gas exchange takes place first through the epidermis and then into the fine peripheral tracheae.

From this point the diffusion pattern is the same as in a spiracular system.

4. Gill Respiration. Among the most conspicuous adaptations for aquatic life are the frondlike gills of damselfly nymphs and mayfly nymphs. These typify many aquatic nymphs and larvae, which have developed gills for their respiratory exchange. The tracheae extend into these gills, and the diffusion of gases takes place through the epidermis between the tracheal threads and the water. An unusual structure occurs in dragonfly nymphs, fig. 144. The rectum is enlarged, and gills provided with abundant fine tracheae extend into the pouch so formed. Into this rectal chamber the insect draws water and then expels it; the respiratory exchange occurs through the thin walls of the gills.

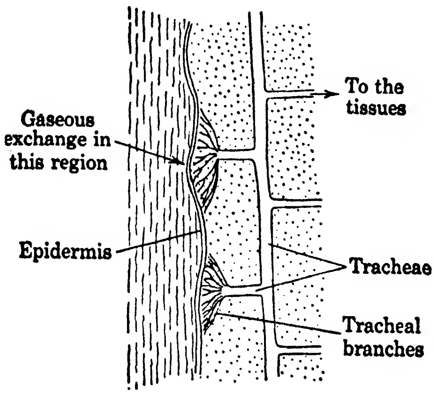


FIG. 143. Diagram of cutaneous respiration in aquatic insects.

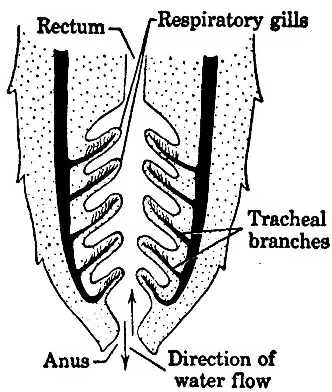


FIG. 144. Diagram of rectal gills of dragonfly nymphs. (Adapted from Wigglesworth)

Respiration of Internal Parasites. The larval forms of many insects feed as parasites within the bodies of other insects. Because they are surrounded by the liquids of their host, they live in what is practically an aquatic habitat. It is not surprising, then, to discover that their respiratory adaptations parallel those of aquatic forms.

Many of the parasitic larvae rely on cutaneous respiration. Extremely small forms may have no tracheal system, but the larger ones have it well developed and have a network of peripheral tracheal strands. Other forms, such as the tachina flies, have functional posterior spiracles which either project through the body wall of the host or are connected internally with one of the host's tracheal trunks.

THE BLOOD AND CIRCULATION

Insects have a supply of blood which is a tissue liquid similar in some respects to mammalian blood. The blood effects the chief distribution of food products to the tissues and carries waste products from them. Normally it has only a secondary although important role in respiration. It flows through closed ducts for only a short part of its course, its progress through the tissues being by percolation. Thus, in both distribution characteristics and circulation method, insect blood resembles mammalian lymph more than mammalian blood. In insects the blood, in addition to the afore-mentioned functions, constitutes a hydraulic-pressure system with its own peculiar functions.

Blood Properties. Insect blood is usually a greenish or yellowish liquid, but may be clear and colorless. Its specific gravity is close to that of water, varying from about 1.03 to 1.05. It is usually slightly acid, but the *p*H varies with the species, instar, age, and sex. The dissolved substances in insect blood include about the same array of salts, proteins, glucose, urea, and fats as mammalian blood, but the proportions are often quite different. The most striking features include a very low chloride content and an extraordinary amount of amino acids, which may be 20 to 30 times as abundant as in human blood.

Insect blood differs greatly in its clotting properties. In many kinds of insects it does not clot at all, and wounds are simply stopped by a plug of cells. In other species the blood clots readily.

Almost without exception the blood contains no hemoglobin and apparently has no mechanism for absorbing oxygen in chemical combination. It will take up oxygen and carbon dioxide in physical solution.

Blood Cells. At first examination the cells in insect blood present a great diversity of shapes. An analysis of these in various insects indicates that usually only two types are represented: *hematocytes* and *enocytoids,* fig. 145.

Hematocytes appear first as small dark-staining bodies incapable of phagocytosis. They become pear-shaped or spindle-shaped when mature and can then ingest tissue debris, dead bacteria, and other particles; at this stage they are termed phagocytes. The hematocytes multiply and grow throughout the insect's life. They assume varied shapes during growth. When they are mature, their shapes are influenced by ingested material. Hematocytes may adhere to tissues, in which case they spread out in a starlike form. In some insects all the hematocytes circulate with the blood fluid; in others all adhere to tissues, forming clusters of phagocytic "tissue"; in many others both circulating and attached phases occur.

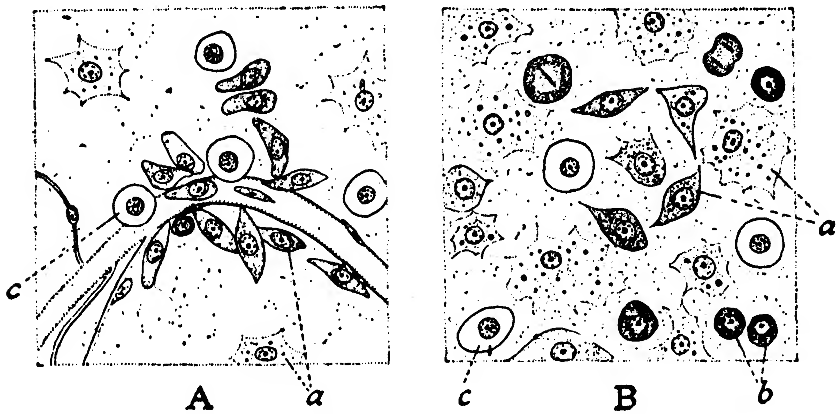


FIG. 145. Hemocytes in the bug *Rhodnius*. *A*, group of hemocytes around trachea where this is passing through the basement membrane of the epidermis; a few are spread out in stellate form on the basement membrane. *B*, hemocytes below the basement membrane at the height of molting; many of the phagocytes contain basophil droplets from disintegrated cells; proleucocytes dividing mitotically. *a*, phagocytes; *b*, proleucocytes; *c*, enocytoids. (From Wigglesworth, "Principles of Insect Physiology," by permission of E. P. Dutton and Co.)

Hematocytes are as varied in function as in appearance. They ingest some living and all dead bacteria, collect at wounds and form a plug to close such breaks in the body wall, and form a partition to exclude certain parasites from the body cavity. In addition, the blood cells frequently play an important part in histolysis during advanced metamorphosis.

Enocytoids are round or oval cells found in the blood of most insects and are most abundant during molting. Unlike hematocytes, they take no part in phagocytosis. Their function is unknown, but they have been noticed collected around zones of phagocytes encasing foreign bodies.

Functions. The blood of insects has four known functions. The first three listed here are functions of the blood as a living tissue, whereas the fourth function is purely mechanical.

1. Transportation. Digested food materials are absorbed from the digestive system and conveyed to the tissues, and waste products are carried from the tissues to the excretory organs. In addition, certain hormones are transported from their source to the tissues.

2. Respiration. Presumably in all insects at least some of the cells are not provided with tracheoles for direct respiratory exchange. These cells undoubtedly obtain their oxygen from the dissolved store in the blood. We have seen that much carbon dioxide diffuses through the tissues and finally through the cuticle; the blood aids this process. In larvae of certain species of *Chironomus* the blood contains dissolved hemoglobin. This is not nearly so effective in absorbing oxygen as mammalian hemoglobin. It does take up considerable oxygen, however, which the larvae use when hiding in the oxygen-deficient ooze on the bottom of a pond.

3. Protection. The hematocytes dispose of certain bacteria and parasites. The healing of wounds is effected by the blood or its hematocytes.

4. Hydraulic Function. The entire volume of blood inclosed within the body wall forms a closed hydraulic system capable of transmitting pressure from one part of the body to another. In this purely mechanical sense it is put to many uses by the body. The pressure of the blood is regulated by contractions of the thorax or abdomen or both. Alternate increase and decrease of blood pressure, brought about by respiratory movements, causes the emptying and filling of the tracheal·air sacs and pouches. Localized blood pressure is responsible for stretching of the exoskeleton after molting, inflation of the wings, and frequently operation of the egg-breaking device at time of hatching.

Circulation. In general, fig. 146, insect blood circulation follows this path: It is pumped forward by the heart from the abdomen, through the aorta, and emptied into the head; from the head it percolates back between the tissues until it reaches the abdomen, where the circle starts forward again through the heart.

Blood is sucked into the heart through the ostia and then driven forward by peristaltic movements which flow along the entire length of the heart. The negative pressure of the heart chambers which aspirates the blood and the systolic pressure which causes the forward flow of blood are due to the elasticity and muscular manipulation of the heart, the aliform muscles, and other muscles which may be associated with them. At times the flow is reversed, and blood pours from the heart back into the visceral cavity. In most insects the heart is unobstructed for its entire length. In a few the ostia are recessed into the heart to form valvelike flaps which divide the heart into segmental chambers.

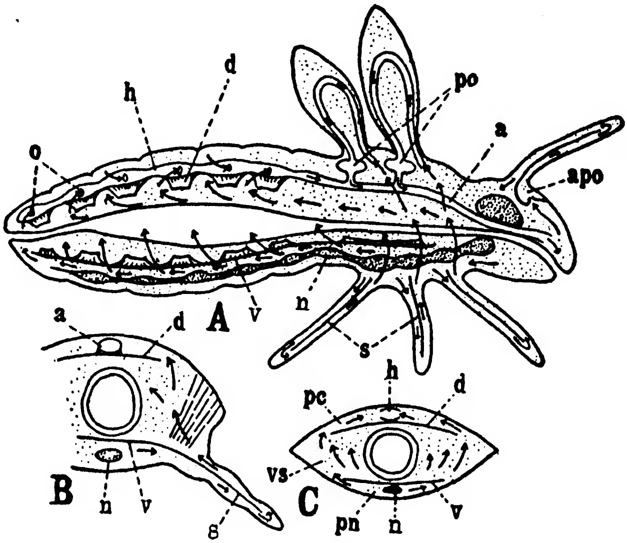


FIG. 146. Circulation accomplished by heart and accessory structures. *A*, insect with fully developed circulatory system, schematic; *B*, transverse section of thorax of the same; *C*, transverse section of abdomen. Arrows indicate course of circulation (based largely on Brocher). *a*, aorta; *apo*, accessory pulsatile organ of antenna; *d*, dorsal diaphragm with aliform muscles; *h*, heart; *n*, nerve cord; *o*, ostia; *pc*, pericardial sinus; *pn*, perineural sinus; *po*, meso- and metathoracic pulsatile organs; *s*, septa dividing appendages; *v*, ventral diaphragm; *vs*, visceral sinus. (From Wigglesworth, "Principles of Insect Physiology," by permission of E. P. Dutton and Co.)

In addition to the heart, a varied assortment of structures exist to aid the blood flow through the appendages or its distribution in the body cavity. In rare cases the aorta may discharge into vessels which carry the blood in different directions. In many insects the antennae and legs are divided by longitudinal membranes so that the blood enters on one side, flows the length of the appendage, and empties on the other side. Blood movements into the appendages are aided also by the respiratory movements, so that the "pulse" in the legs may synchronize with respiratory contractions and not with the heartbeats.

There are frequently supplemental blood pumps, or pulsatile organs, in the meso- and metathorax for sucking blood through the wings. In these instances the blood flows through certain veins of the wings, fig. 147, and is returned either directly to the aorta or to the body cavity. When well developed, the ventral diaphragm also assists blood flow; contractions of the diaphragm muscles drive the blood both laterally and backwards.

The diagrams in fig. 146 outline the direction of flow set up by these various methods.

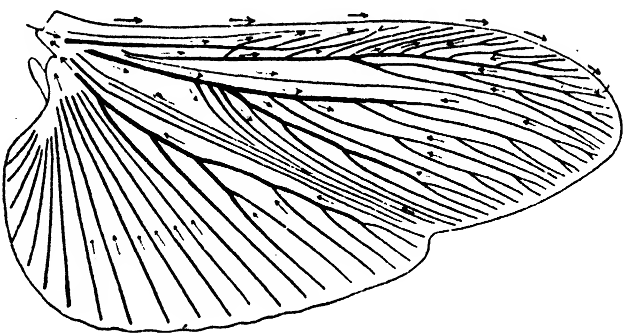


FIG. 147. Hind wing of the cockroach *Periplaneta americana,* with the course of circulation of the blood indicated by arrows. (From Wigglesworth, after Yeager and Hendrickson)

The heart is so well supplied with nerves from both the visceral nervous system and the segmental ganglia that many investigators believe all its activities are controlled by nerve impulse. It is still a moot point, however, as to whether the automatic heartbeats are due to nerve stimulation or to muscle which possesses the ability to contract and relax periodically without nervous stimulation.

REPRODUCTION

In insects reproduction is the function of the sexual reproductive system. Normally insect reproduction is bisexual, in that the egg produced by the female will not develop unless fertilized by spermatozoa produced by the male. Except in a few species, only one sex is represented in any one individual. In most insect species, therefore, the physiology of reproduction deals with the development and maturation of spermatozoa in the male and of eggs or ova in the female and the manner in which they are brought together.

Development of Spermatozoa. Spermatozoa are produced in the follicles of the testis, fig. 148. The upper portion of the follicles contain primary germ cells called spermatogonia. These divide repeatedly to form cysts, which move to the base of the follicle due to the pressure of their own increase in size. At the base of the follicle each cell in a cyst undergoes repeated division and may increase in number 5 to 250 times. In the next cell division following this multiplication stage there occurs the reduction division of the chromosomes. This is followed by a transformation period in which the round cells develop into slender flagellate spermatozoa. These mature sperms escape from the duct of the follicle (*vas efferens*) into the genital ducts (*vas deferens*); they are stored in an enlarged or coiled portion of this duct, the seminal vesicle, until mating. At the time of mating the spermatozoa are transferred to the spermatheca of the female, where they are stored until needed for fertilization.

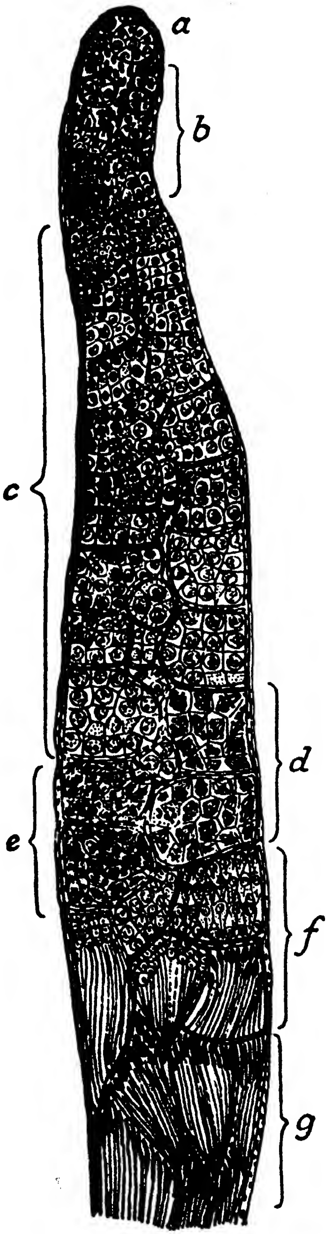


Fig. 148. Longitudinal section of testis follicle of a grasshopper, semischematic. *a*, apical cells surrounded by spermatogonia; *b*, zone of spermatogonia; *c*, zone of spermatocytes; *d*, cysts with mitoses of second maturation division; *f*, zone of spermatids; *g*, zone of spermatozoa. (From Webber after Depdolla)

Development of Eggs. The eggs are developed in the ovarioles of the ovary. The tip of the ovariole, the *germarium*, contains primary germ cells which divide to produce developing eggs, or oöcytes. These usually appear in successive stages of growth down the length of the ovariole. The oöcytes derive nourishment for their growth from either the follicular epithelial cells forming the ovariole, fig. 149*A* or from special "nurse cells" present in the ovariole, figs. 149*B* and *C*. Below the oöcyte at the end of the ovariole is a plug of epithelial cells which seals the duct leading from ovariole to oviduct. When the oöcyte is fully developed, this plug breaks down, and the oöcyte or egg is released into the ovi-

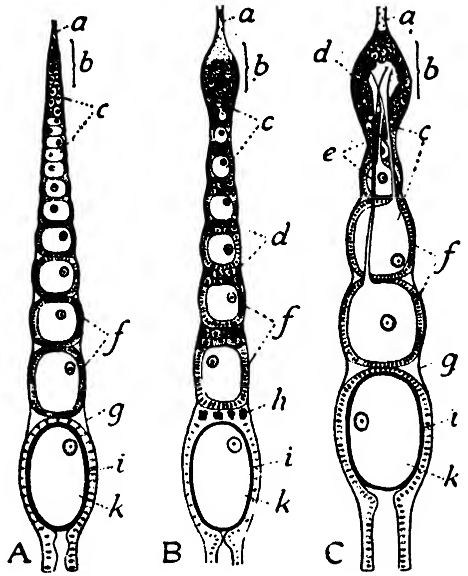


FIG. 149. Longitudinal section of ovarioles. *A*, simple or panoistic type having only oöcytes; *B*, polytrophic type having oöcytes and nurse cells alternating; *C*, teleotrophic type having nurse cells connected to oöcytes by nutritive cords. *a*, terminal filament; *b*, germarium; *c*, oöcytes; *d*, nurse cells; *e*, nutritive cords; *f*, follicular cells; *g*, peritoneal coat; *h*, degenerated nurse cells; *i*, chorion; *k*, egg. (From Wigglesworth after Weber)

duct. The portion of the ovariole which contained the released egg shrinks, and a new plug forms below the next oöcyte. As this oöcyte matures and its chamber enlarges, it assumes the same position as the previously discharged egg.

The eggs at time of discharge into the oviduct are surrounded by the eggshell or chorion. The eggshell is perforated in one or more places by a minute pore or micropyle. It is through these minute openings that the spermatozoa gain entrance to the interior of the egg.

Fertilization. As the eggs pass down the oviduct (by peristaltic action of the oviduct muscles) into the vagina, they come to lie at the opening of the spermathecal duct. From this duct spermatozoa emerge and enter the egg micropyle. After the spermatozoa enter the egg, the egg nucleus undergoes two divisions, one a reduction division, with the production of the female pronucleus and polar bodies. The spermatozoan loses its tail and changes to the male pronucleus. The male and female pronuclei unite to form the zygote.

From this usual sequence of events there are many deviations. The following are interesting examples. In the bedbug *Cimex* the spermatozoa migrate from the spermatheca, into the follicular structure of the ovarioles and from there into early-stage oöcytes. Fertilization is thus accomplished before the eggshell is formed. In parthenogenetic species such as the European spruce sawfly *Diprion hercyniae,* fertilization does not occur, but the diploid chromosome count is restored by fusion of a polar body with the female pronucleus.

Mating. At each mating a large number of spermatozoa are transferred from the male to the female. The female stores and controls the spermatozoa so that only a small number are liberated at a time as successive eggs pass down the oviduct. In this way a separate mating is not necessary for the fertilization of each egg. As a consequence a large number of insects mate only once in their lifetimes, and most of the remainder mate only a few times.

Mating is induced by stimuli of many kinds; by peculiar movements, such as the dancing of swarms of male mayflies; by sound, as the chirping of crickets and grasshoppers; by color reactions, as in some butterflies; and chiefly by a wide variety of scents. The gonads seem to have no marked influence on mating behavior, since many species mate before the female ovaries are well developed, and castrated males will mate normally but without transfer of spermatozoa.

The mechanics of spermatozoa transfer may be divided into several distinctive types. In many forms, such as some of the true bugs, the penis is inserted into the female spermatheca and the spermatozoa placed directly in this storage chamber. In many moths, grasshoppers, and beetles, the penis discharges the spermatozoa into the female bursa copulatrix; after mating, the spermatozoa become transferred from this structure to the spermatheca. The mechanism of this transfer is not known. In many insects of this group having a bursa copulatrix, the spermatozoa are transferred in a membranous sac or *spermatophore,* formed by the secretion of the male accessory glands. This sac of spermatozoa is deposited in the bursa or vagina, and its contents are transferred to the spermatheca. After this transfer the empty spermatophore is ejected by the female.

Longevity of Spermatozoa. Apparently the secretions of the female spermatheca or its associated glands can keep spermatozoa viable for a considerable period. The honeybee can sustain its spermatozoan store for several years. In moths the spermatozoa remain alive in the spermatheca for several months. In females of a few insects, such as the bedbug *Cimex,* the spermatozoa not utilized in a few weeks are digested and absorbed by the body tissues, and mating occurs from time to time to replenish the supply.

IRRITABILITY

A characteristic of living organisms is their ability to respond to stimuli, a property called irritability. In a general way irritability is the protective function by which the organism can move away from harmful environmental conditions or toward more favorable conditions. From the standpoint of mechanical performance, three definite functions are embodied in irritability. These are *sensitivity,* the ability to detect or perceive stimuli; *conductivity,* the transmission of stimuli from the point of reception to various parts of the body; and *contractility,* the power of contraction, on which depends the organism's ability to make a response to the original stimulus.

In primitive forms of unicellular life all three of these functions are performed by the same cell. Sensitivity lies in the cell membrane; conductivity and contractility are apparently properties of the general protoplasm. In highly organized animals each of these functions is performed by special structures or tissues. Insects have a well-developed system for accomplishing these various components of irritability. Sensitivity is seated in sense organs, some simple and some complex, distributed over various parts of the body. These receive stimuli. Conductivity is performed by the nervous system, which "telephones" notice of stimuli from the sense organs to reacting tissues. Contractility is accomplished by various cells or tissues especially modified for this purpose, notably muscle tissue and certain glands. When activated by "messages" coming over the nerve fibers, contractions of the muscles or secretion of hormones by the glands cause a reaction, or response, to the stimuli detected by the sense organs.

In observations on behavior, the terms *reception* and *response* are usually employed. These terms pertain to the two ends of the irritability chain, emphasizing the stimulus received and the response given by the organisms.

Sensitivity

Sensitivity of the organism as a unit is centered in specialized cells or groups of cells termed sense organs. These serve for the reception of many external types of stimuli, including tactile, auditory, gustatory (taste), olfactory (smell), and visual. In addition, insects respond definitely to temperature changes, hunger, and internal physiological conditions; no special receptors are known for these senses. Insects also exhibit an acute orientation to gravity (geotropism), but their method or methods of accomplishing this are little understood.

Nerve fibers have no selectivity. They transmit only an abstract impulse. In order to acquaint the central nervous system with the nature of different stimuli, sensory areas have been developed, each one responsive to only one type of stimuli, and each with its separate nerve endings. The nervous system is therefore able to identify types of stimuli by the location from which the impulses come.

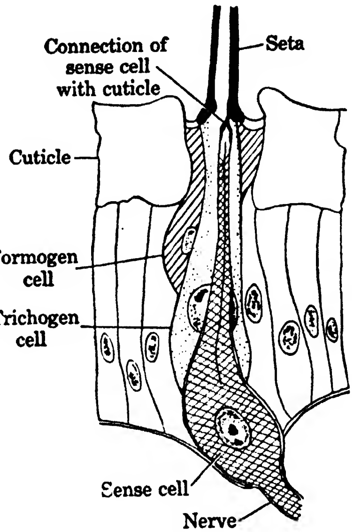


FIG. 150. A simple hairlike sense organ. (Redrawn from Snodgrass)

The actual structures which serve as sense receptors vary from simple types to extremely complex organs such as the compound eyes.

Structure of Sense Receptors. Hairlike sense organs are the simplest type. They are typical setae to which have been added nerve cells and nerve endings, fig. 150. The nerve ending is set at the base of the seta in such a manner that the movements of the seta change the pressure on the tip of the nerve ending. Such changes of pressure cause a definite impulse to be transmitted along the nerve fiber. These hairlike sense organs usually serve for tactile stimuli. A great variety of organs for reception of stimuli relating to taste or smell are similar in general structure to these hair organs. They differ in that the hair has been replaced by a thin-walled peg, fig. 151*A*; a plate; or a dome, fig. 151*B*; with which part the tip of the nerve ending is in contact. Some of these sense organs may have a group of sense cells associated

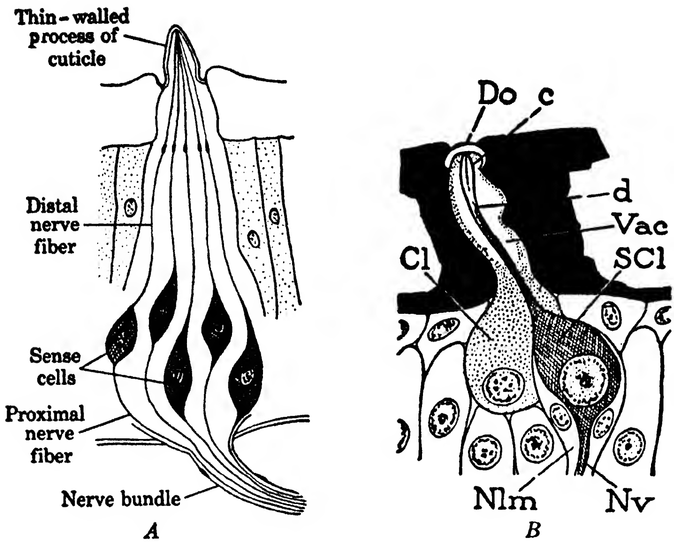


FIG. 151. Sense cells and their receptors. *A*, chemoreceptor having thin walled peg and multiple sense cells. *B*, domelike sense receptor (*Do*) on cercus of a cockroach. *c*, connection of nerve with cuticle; *Cl*, trichogen cell; *d*, distal part of nerve; *Nlm*, nerve sheath; *Nv*, nerve; *Scl*, sense cell; *Vac*, vacuole. (After Snodgrass; *A*, redrawn)

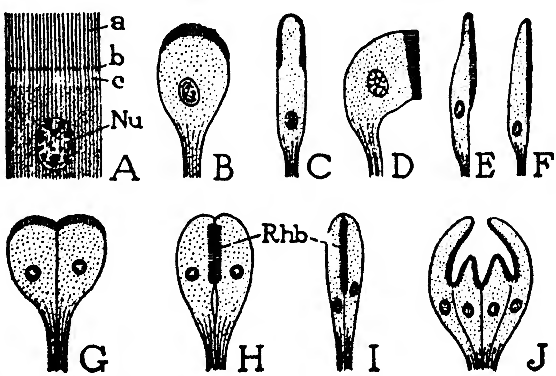


FIG. 152. Diagrams of light receptor cells and the development of a rhabdom. *A*, receptive pole of a sense cell; *a*, striated zone (rhabdomere) formed of ends of neurofibrillae; *b*, basal bodies; *c*, clear zone (from Hesse). *B–J*, different positions of the striated zones on ends of sense cells. *H*, *I*, union of the striated zones of adjacent cells to form a rhabdom (*Rhb*). (*B–J* from Weber.) (After Snodgrass)

with the peg or plate, allowing the accommodation of several nerve endings in the same receptor, fig. 151*A*.

Eyes. Visual organs or eyes occur in most insects and consist of aggregations of photoreceptive cells. Photoreceptive sense cells are extremely varied in histological detail. They differ from other types of sense cells in two features: (1) The cuticle overlaying them is transparent, forming a *cornea,* and (2) the sense cells have no definite tip, but instead contain fine surface striations which are apparently the sensitive receptive elements of the cell, fig. 152*A*.

Insect eyes may be divided conveniently into two types: simple and compound. The simple types have a single lens for the entire eye, fig. 153. The lens is specialized cuticle secreted by a layer of epithelial cells called the corneagenous cells, which are themselves transparent. Nerve cells form a retina beneath the corneagenous layer. In most eyes the striated sensitive elements of the sense cells have migrated to form a line down one side of the cells. The cells are frequently oriented so that these "lines" of adjacent cells are together. The linear compound sensitive element so formed is called a *rhabdom,* fig. 152*H, I*.

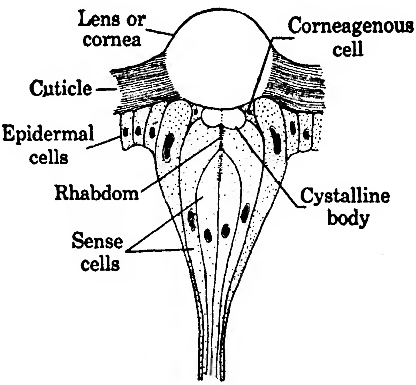


FIG. 153. The simple eye of a caterpillar. (Redrawn from Snodgrass)

Compound eyes have the same basic parts as simple eyes, but the sense cells are grouped into concentric units called *ommatidia.* Each ommatidium, fig. 154, has its own lens (distinguished externally as a *facet*), sometimes a lenslike cone, below this a rosette usually of eight sense cells with a central rhabdom, and pigment cells around both cone and rosette. The pigment cells contain colored granules which can move up and down in the cell. This movement is synchronized in all the pigment cells surrounding an ommatidium and controls the amount of light reaching the sensory portion of the ommatidium.

In adult insects the ocelli are simple eyes, and the large lateral faceted eyes are compound. Larvae have only simple eyes; sometimes several of these form a cluster. Both types of eye connect as a unit directly with the brain.

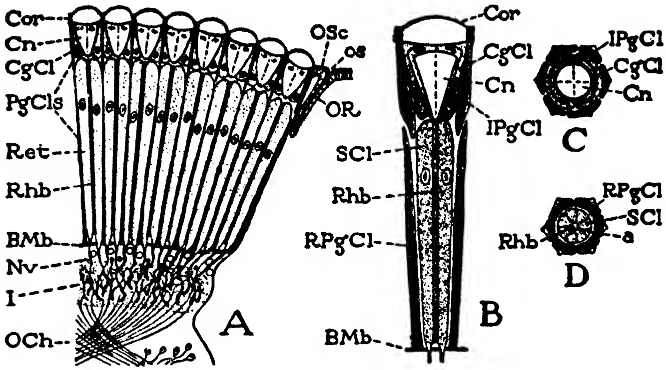


Fig. 154. Diagram of a compound eye, and of an ommatidium. *A*, vertical section of part of eye. *B*, typical structure of an ommatidium. *C*, horizontal section of ommatidium through cone. *D*, same through retinula. *a*, eccentric retinula cell; *BMb*, basement membrane (membrana fenestrata); *CgCl*, corneagenous cell; *Cn*, crystalline cone; *Cor*, corneal lens; *I*, lamina ganglionaris; *IPgCl*, iris pigment cell; *Nv*, nerve; *OCh*, outer chiasma; *OR*, ocular ridge; *os*, ocular suture; *OSc*, ocular sclerite; *PgCls*, pigment cells; *Ret*, retinula; *Rhb*, rhabdom; *RPgCl*, retinal pigment cell; *SCl*, sense cell (retinula cell). (After Snodgrass)

Conductivity

In insects, as in all the higher Metazoa, the basis of conductivity is the nerve cells. But these cells have become sufficiently developed into different types that they act also in the capacity of coordination or association.

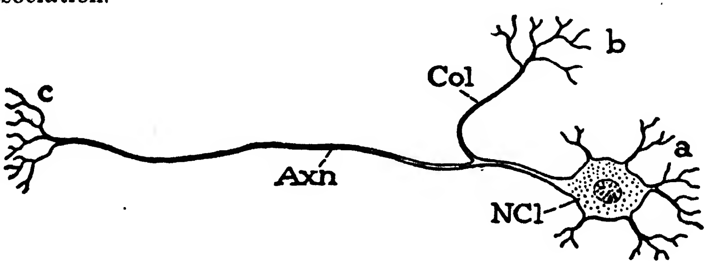


Fig. 155. Diagram of a nerve cell or neurone. *a*, dendrites of the cell body; *Axn*, axon, or neurite; *b*, *c*, terminal branches or arborizations; *Col*, collateral branch of the axon; *NCl*, the cell body, or neurocyte. (After Snodgrass)

Nerve Cells. A nerve cell, or neurone, fig. 155, is composed of three principal parts: a *nucleus*, a long nerve fiber or *axon*, and a branch of the axon called a *collateral branch*. Impulses or stimuli are received by the tips of the collateral branch and travel to the tips of the axon.

This direction is not reversible. Impulses may be passed from one nerve cell to another through a *synapse,* an area in which are intermingled the end fibrils of the axon of one cell and of the collateral branch of another. Three types of nerve cells are used in the more generalized reactions: (1) sensory nerve cells, with the fibrils or tip of the collateral branch intimately associated with a sense organ; (2) association nerve cells, which receive impulses from sensory cells and pass them on either to motor cells or to still other association cells; and (3) motor nerve cells, which receive impulses from association cells and transmit them to glandular or muscle cells. This causes these latter cells to secrete or contract, respectively, and the original impulse has run its course.

Coordination. The synapses of each body segment are grouped together to form the ganglia of the central nervous system. Thus the sensory nerves all "report" to these centers, and the "orders" go out from these to the reactive tissues. Association cells run from ganglion to ganglion, and into the brain. They also may link the same motor cell to several sensory cells or several motor cells to one sensory cell. This whole communications system coordinates responses in different parts of the body with stimuli received at only one station. Thus a touch on a cockroach's cercus (reporting to the terminal abdominal ganglion) will cause the animal's legs (motivated by the thoracic ganglia) to respond with running movements.

Contractility

As previously noted, the function of contractility in insects includes muscle reaction, resulting in movement, and glandular reaction, resulting in hormone secretion. Muscle tissue is the more conspicuous type, and its contractions are responsible for movements of the insect as a whole and its internal and external parts individually.

1. Muscular Reaction. Insect muscles are similar to those of other animals in that they are elongate and have the power of contraction when stimulated by an impulse from a nerve cell. The period of contraction is followed by a period of recovery in which the muscle cell returns to its original shape. Insect muscles are striated, and the individual muscle cells are grouped together to form bundles or fibers which act as a unit, fig. 156. In anatomical usage it is these bundles which are called muscles.

Muscular contraction results in the movement of some part. For every movement there is a countermovement, in which the part regains its normal position. This countermovement is frequently brought about by the action of a second muscle, as in fig. 157*A*. Here the

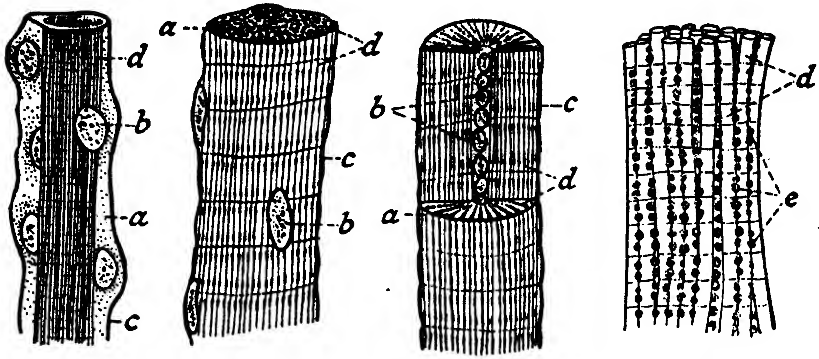


FIG. 156. Insect muscle fibers. *A*, from larva of honeybee; *B*, from leg muscles of a scarab beetle; *C*, from leg muscles of honeybee (tubular muscles); *D*, indirect flight muscles of honeybee (a group of sarcostyles from fibrillar muscle). *a*, sarcoplasm; *b*, nuclei; *c*, sarcolemma; *d*, fibrils or sarcostyles; *e*, sarcosomes. (From Wigglesworth after Snodgrass)

tibia articulates at each side with the femur at the point *l*; contraction of the elevator muscle *lv* raises the tibia for the initial movement; contraction of the depressor muscle *dpr* lowers the tibia for the countermovement. In other cases only a single muscle is involved. In these

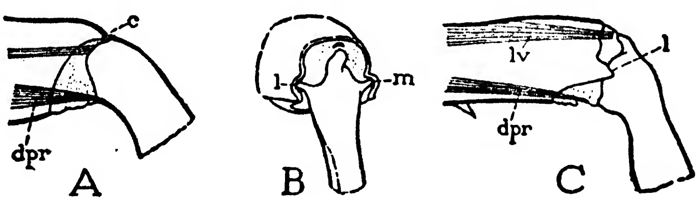


FIG. 157. Movement of an adult insect leg. *A*, monocondylic (single socket) joint (*c*). *B*, *C*, dicondylic (double socket) joint, (*l* and *m*), end view and side view with levator (*lv*) and depressor (*dpr*) muscles. (After Snodgrass)

the countermovement is brought about either by the pressure of the blood or by tension of flexible membranes. In countermovement by blood pressure, the hydraulic pressure of the blood simply forces back the part when muscle tension is released.

Flight. The muscular mechanism for insect flight is of unusual interest because nothing at all like it is found in any other animal group. Flight is attained by the stroking of the wings, which are essentially outgrowths of the lateral margin of the meso- and meta-thoracic tergites. In the dragonflies, damselflies, lacewing flies, and other primitive orders, the two pairs of wings move independently. In the damselflies, for example, as one pair of wings goes up, the other pair goes down. In the moths and butterflies, bees and wasps, and certain others, the two wings on a side are held together or coordinated by various types of hooks, bristles, or folds, so that both pairs work in unison. In the beetles and some of the true bugs, the front wings form hard armor plates, and only the hind wings function in flight. In the twisted-winged insects (Strepsiptera), the front pair is reduced, and in the true flies (Diptera), the hind pair is reduced, so that each of these two orders has only a single pair of flight wings.

Wing movements producing flight are controlled by about six to a dozen pairs of muscles. The exact muscle arrangement differs in various orders. These muscles act on the notum, basalar and subalar sclerites, and the axillary sclerites, but are not connected directly with the wing itself. In spite of the seeming complexity which would appear to attend insect flight, the wing movements are produced by a very simple seesaw or leverage arrangement.

The principal points and parts involved are these, fig. 158*A*:

1. The wing is attached intimately to the edge of the central portion of the notum. A hinge joint *j* is present along the line of attachment.

2. The center of the notum can be moved up and down by muscle action, carrying the base of the wing with it.

3. The wing, just beyond its base, passes over the pleural process *p*, which is the pivot or fulcrum of the wing seesaw. As far as a consideration of flight is concerned, this pivot point is stationary.

Thus, fig. 158*B*, when the set of powerful muscles connecting the sternum and notum contract, the notum is pulled down and pulls the wing base with it. The pivot point does not move, so that the expanded part of the wing beyond the pivot is raised at an angle proportionate to the lowering of the wing base. This causes the upstroke. As the sternonotal muscles relax, another set of muscles contract. These latter muscles, fig. 158*C, D*, connect the front and hind margins of the notum, like a bowstring. When they contract, fig. 158*D, E*, the "bow" or notum is arched, causing the central portion to elevate, carrying the base of the wing upward with it. This causes the downstroke and produces the other half of the seesaw motion. Figures

158*A*, *B*, *C*, *D*, and *E* are greatly exaggerated to illustrate the points made; in reality the distances involved are minute, and the accessory musculature is complex.

The deflection of the wing is caused by other muscles which, acting on the axillary sclerites, can pull down the front margin of the wing. In this movement the pleural process is used again as the fulcrum or pivot point.

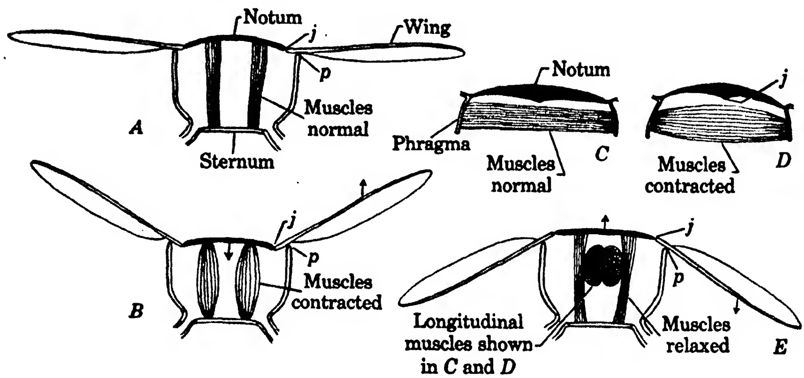


FIG. 158. Diagrams of muscles and movements producing insect flight. *j*, attachment of wing to notum; *p*, pleural process which acts as a pivot point for the "seesaw" of the wing. *A* and *B* are cross sections that show only the vertical muscles connecting notum and sternum; when these muscles contract, as in *B*, the notum is pulled down, depressing the edge of the wing, which pivots at *p*, forcing upwards the major portion of the wing. *C* and *D* are longitudinal sections of the mesonotum that show the longitudinal muscles; when these contract, as in *D*, they "bow" the notum, causing the center to raise. The effect of this is shown in cross section *E*; the raised edges of the notum at *j* carry up the ends of the wing, which pivots again at *p*, and this forces downward the projecting wing.

Flight Speed and Direction. In flight three types of wing movements are produced: (1) an upstroke and downstroke, (2) a deflecting or tilting, and (3) a forward and backward swing. All three types occur simultaneously but to different degrees, depending on speed and wing size.

The up-and-down stroke alone produces little more than elevation. Thus in butterflies which rely chiefly on this stroke, flight is mostly fluttering, with very little speed in a forward direction. Addition of the deflecting movements decreases the air pressure in front of the wing and increases the air pressure behind it, in the same manner as an airplane propeller. The pressure behind pushes the insect forward at the same time that the partial vacuum in front pulls it forward. Deflection is therefore the principal agent in forward movement. Insects with highly developed deflection, such as dragonflies, are able to maintain a steady forward flight.

Rate of stroke varies exceedingly with different species. The slowest group is exemplified by the butterflies; the cabbage butterfly makes about 10 strokes per second. Faster rates are made by the honeybee, with 190 strokes per second, the bumblebee with 240, and the housefly with 330.

Greatest speed is attained by a combination of great deflection, a long narrow wing, and usually at least a fairly high rate of stroke. Fastest recorded flight of insects is developed by the sphinx moths (Sphingidae), attaining a rate of over 33 miles per hour; the horsefly (*Tabanus*) with a rate of over 31 miles per hour; and the dragonfly, which cruises at about 10 miles per hour but can speed up to about 25.

In forward flight, the path of the wing makes a figure "8" which leans forward at the top of the wing stroke. Many insects such as the hover flies (Syrphidae), bees, and many flower-visiting moths, are able to fly backwards; this is done by reversing the path of the wings so that the figure "8" leans back at the top of the stroke.

2. Glandular Reaction. Inconspicuous but highly important are hormone glands. Experimental work on insects has indicated for some time that important activities, such as molting and metamorphosis, may be controlled by these secretions. There is evidence also that color tones of certain kinds may be controlled in the same way. In *Pieris* pupae, for instance, it appears that color reception by the pupal eye controls a hormone which affects pigmentation of the epidermis and brings about a pupal color tone which matches that of its surroundings. Exactly where all hormones are produced in the insect is not known. Decapitation and ligaturing experiments have proved the head region to be the source of many. Recent histological and extirpation experiments indicate that at least some hormones are produced by the corpora allata, which are small structures closely associated with the brain. Extirpation experiments in the Crustacea suggest strongly that in these groups (and presumably in insects also) many parts of the brain itself secrete distinctive hormones in response to external stimuli.

It is conceivable, therefore, that the brain (together with the associated corpora allata) may be in part its own hormone dispensary and may exercise much of its control through these secretions. Such an arrangement would be advantageous in more ways than one. Hormone production would be located at or near the center of stimulation;

the hormones would enter the blood stream at its most concentrated point and would be carried rapidly to all parts of the body; and such an arrangement would eliminate the necessity of adding other association and motor units to the ventral nervous system.

This does not eliminate the possibility that hormones are produced in other parts of the body. Study of the endocrine processes of insects is still in its infancy.

BEHAVIOR

Insect behavior is the manner in which insects conduct themselves: in other words, what they do, when they do it, and why. A great amount of work has been done on the study of insect behavior. Most of these studies probe the question of behavior from one of two approaches. One is the individualistic approach. Experimentation, especially training criteria, has established the recreation of many insects to various qualities and quantities of light, odors, tastes, sounds, touch, and other stimuli. The reactions and adjustments of an individual to abnormal situations have resulted in information on learning ability and the orbit in which instinct and intelligence overlap.

The second approach deals with the behavior characteristics of the species. The entire life cycle of an insect (or any other organism) is a succession of definite behavior patterns. Even in the same species they change constantly and regularly. Thus the larva of the June beetle shuns light, but the adult is attracted to it; certain cutworms move down into the soil during the day but climb plants at night for feeding. Cocoon formation and mating represent behavior patterns which appear and persist for only a very short period of the insect's life cycle.

The basic units of inherited behavior are reflex actions, that is, automatic responses to the same stimulus. When the entire organism orients itself automatically in relation to a given stimulus, this is known as a tropism. For instance, at night certain species of moths will always fly towards a flame, exhibiting a positive tropic response to light. Tropisms which are inherited and therefore operate without benefit of experience are called instincts. Insect behavior in general is predominantly instinctive, but it is not a simple addition of reflexes, tropisms, and instincts. In the first place, these may be modified, inhibited, or coordinated as a result of experience or learning. In the second place, many investigators believe that the entire perceptual panorama of the organism forms a sort of pattern and that the organism responds to general changes in this pattern and not to the individual stimuli of which the pattern is composed.

There is also an intangible feature of behavior which is well expressed by the following quotation from Wigglesworth: "When we consider the behavior of insects under natural conditions, we find them gaining their ends by an infinite variety of sensory impressions. Inborn reflexes, and reflexes 'conditioned' by the experience of the individual, certainly occur; but these are masked by inhibitions, and integrated by higher centers, in such a way that they serve constantly the needs and purposes of the insect as a whole. It is this unifying quality, that welds the organism together, and makes the whole something greater than the sum of the parts, which in the sphere of behavior as in the sphere of growth still eludes physiological analysis."

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6

The Life Cycle

The start of growth within an egg signals the beginning of a long series of changes leading ultimately to the attainment of adulthood and to production of eggs or young for another generation. This chain of events, from egg to completed adulthood, constitutes the life cycle of the individual. In the Insecta there are many types of life cycle, involving different methods of development, different relations of one generation to another, and a possible alternation of food or abode between different divisions of a single life cycle. In social insects, contemporaneous members of a population living in the same colony may have different features of the cycle.

DEVELOPMENT

The life cycle of the individual is usually considered as two phases, development (from egg to adult), and maturity or adulthood. Development is a period of growth and change which is fundamentally gradual and continuous throughout its course. On the basis of external manifestations, however, it is broken into definite segments or eras. Because most insects start as eggs, the most universally important division point of insect development is the phenomenon of hatching from the egg. The development period within the egg is *embryology;* the period after hatching is the *postembryonic development.* Change of form during this latter period is termed *metamorphosis.*

Embryology

The egg, or ovum. Insect eggs are of many shapes, fig. 159; many of them are simple smooth ellipses; others may be ribbed or sculptured in various ways; other are provided with processes of different kinds, such as the lateral floats of *Anopheles* eggs, fig. 159*G*, which keep them afloat on water.

A typical egg, fig. 160, is a cell encased in two coverings. The outer covering is a tough shell, the *chorion*, which has one to several

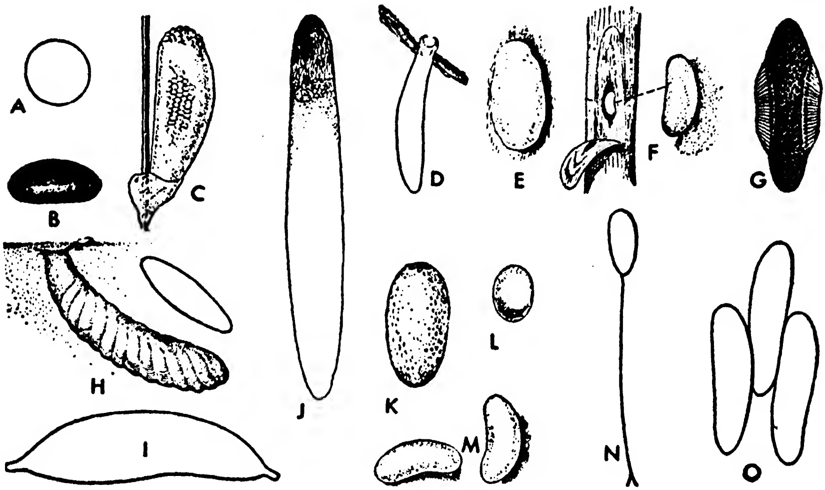

FIG. 159. Eggs of insects. *A*, a collembolan *Sminthurus viridis; B*, an aphid *Toxoptera graminum; C*, the sucking cattle louse *Solenopotes capillatus*, attached to a hair; *D*, apple mirid *Paracalocoris colon*, in plant tissues; *E*, the ladybird beetle *Hyperaspis binotata; F*, a weevil *Sphenophorus phoeniciensis; G*, a malarial mosquito *Anopheles maculipennis; H*, grasshopper egg pod in the soil and a single egg pod; *I*, an ichneumon fly *Diachasma tryoni; J*, a damselfly *Archilestes californica*, removed from water plant; *K*, webbing clothes moth *Tineola bisselliella; L*, dog flea *Ctenocephalides canis; M*, pear thrips *Taeniothrips inconsequens*, removed from tissues of plant; *N*, a lacewing *Chrysopa oculata; O*, housefly *Musca domestica*. (After Essig from various authors)

minute pores, or *micropyles*, through which the spermatozoa enter the egg. Within this chorion is a delicate enveloping membrane, the *vitelline membrane*, surrounding the large nucleus and mass of cytoplasm. The cytoplasm consists of a large central area of yolk (essentially a food store), and a peripheral or cortical layer which is denser than the central part and relatively free from yolk.

Early Cleavage. In the order Collembola the entire egg divides during the early cleavages. As far as is known, this order is the only one in the Insecta which has holoblastic cleavage. In other insects only the nuclei divide during the early cleavages (meroblastic cleav-

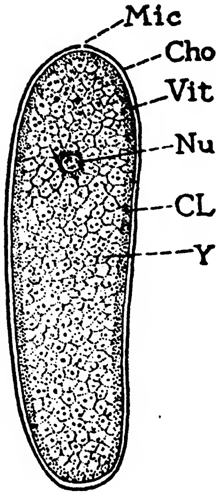

FIG. 160. Section of a typical insect egg, showing its internal structure. *Cho*, chorion, or outer shell; *CL*, cortical layer of protoplasm; *Mic*, micropyle; *Nu*, nucleus; *Vit*, vitelline membrane; *Y*, yolk. (After Snodgrass)

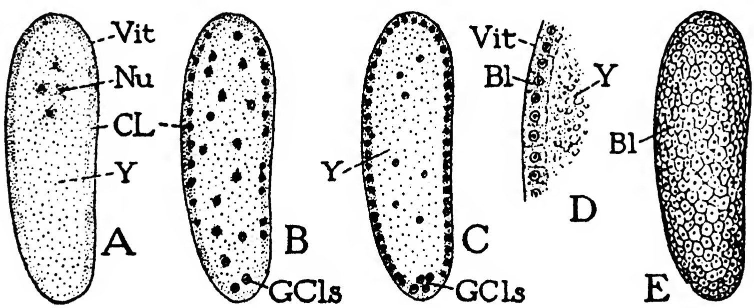

FIG. 161. Early cleavages and formation of the blastoderm. *A*, development begins with the division of the egg nucleus into several cleavage nuclei (*Nu*) within the yolk (*Y*). *B*, the multiplying nuclei migrate outward into the cortical layer of protoplasm (*CL*); several at the posterior pole of the egg become the germ cells (*GCls*). *C*, the nuclei in the cortical protoplasm soon form a definite layer at the surface of the egg; a few nuclei remain in the yolk; the germ cells increase in number. *D*, the cortical protoplasm condenses about each surface nucleus to form a layer of cells, the blastoderm (*Bl*) surrounding the yolk beneath the vitelline membrane (*Vit*). *E*, the blastoderm in surface view. (After Snodgrass)

age); because this is the common method of cleavage in insects, it is the one chosen to illustrate generalized insect embryology.

The nuclei produced by the early cleavages are at first scattered throughout the yolk, fig. 161*A* and *B*, and frequently several of them cluster together in nuclear aggregates. After many nuclei have been formed, most of them migrate from the yolk into the cortical layer, fig. 161*C* to *E*, where each nucleus becomes invested with cytoplasm and a cell wall. These cells make a wall around the egg, one cell thick. In the ventral region, the cells are crowded together to make a thicker

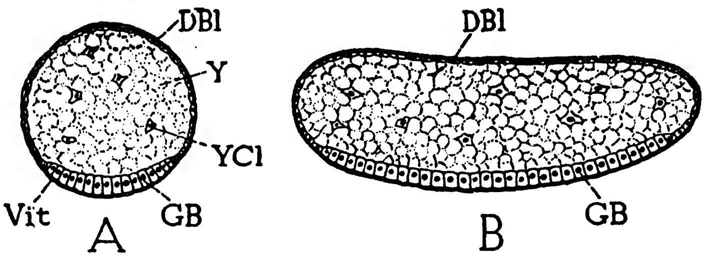

FIG. 162. Diagrams of the formation of the germ band (*GB*) on the ventral side of the blastoderm. *A*, cross section. *B*, longitudinal section. *DBl*, thin dorsal portion of the blastoderm; *Vit*, vitelline membrane; *Y*, yolk; *YCl*, yolk cells. (After Snodgrass)

area, the ventral plate or *germ band*, fig. 162. This is the first organized form of the embryo. In some cases it is quite extensive, extending over a considerable area of the egg. In others it forms only a small platelike area that may be termed a germ disc rather than a germ band. Certain groups of nuclei remain in the yoke and apparently act as a digesting agent, converting the yolk into a form which can be absorbed by the growing embryo. The series of changes from early cleavage to the formation of the germ disc are shown in fig. 163.

Growth of the Embryo. The germ band grows by cell multiplication and differentiation. At first growth is largely an increase in the size of the germ disc, but this is followed rapidly by a surface partitioning whereby the body segmentation and appendages are set out. This is illustrated in fig. 164 which portrays graphically the gross changes leading to the formation of the completed embryo and the first-stage nymph, fig. 165.

Segmentation and Appendages. The development of these two features in the embryo parallels to a considerable extent the supposed evolutionary history of the insect group.

The body segments are first formed in the embryo by a series of transverse incisions, fig. 164, IV. The segments which ultimately bear the mouthparts and fuse with the head structure appear originally

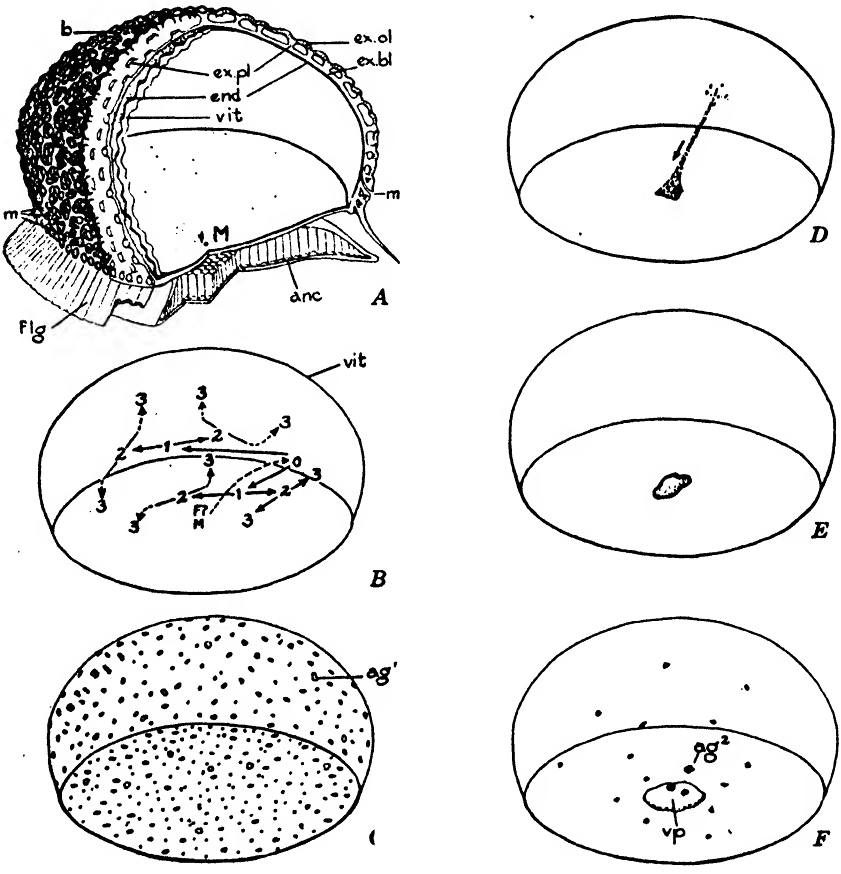

Fig. 163. Steps in the formation of the germ disc in a stonefly egg. *ag*¹, *ag*², primary and secondary nuclear aggregates; *anc*, anchor base; *b*, boss; *ex bl*, *ex ol*, basal and outer layers of exochorion; *ex pl*, pillars in exochorion; *F?*, probable place of fusion of male and female pronuclei; *flg*, flange; *M*, place of maturation; *vit*, vitelline membrane; *vp*, ventral disc or germ plate. Numbers in *B* indicate cleavages and movement of nuclei. (After Miller)

as similar to the posterior segments. It is not until the appendages are well developed that the mandibular, maxillary, and labial segments become fused with the head structure, fig. 164, VII.

Appendages begin to develop soon after segmentation is evident, fig. 164, V. Typically each segment develops a pair of ventral ap-

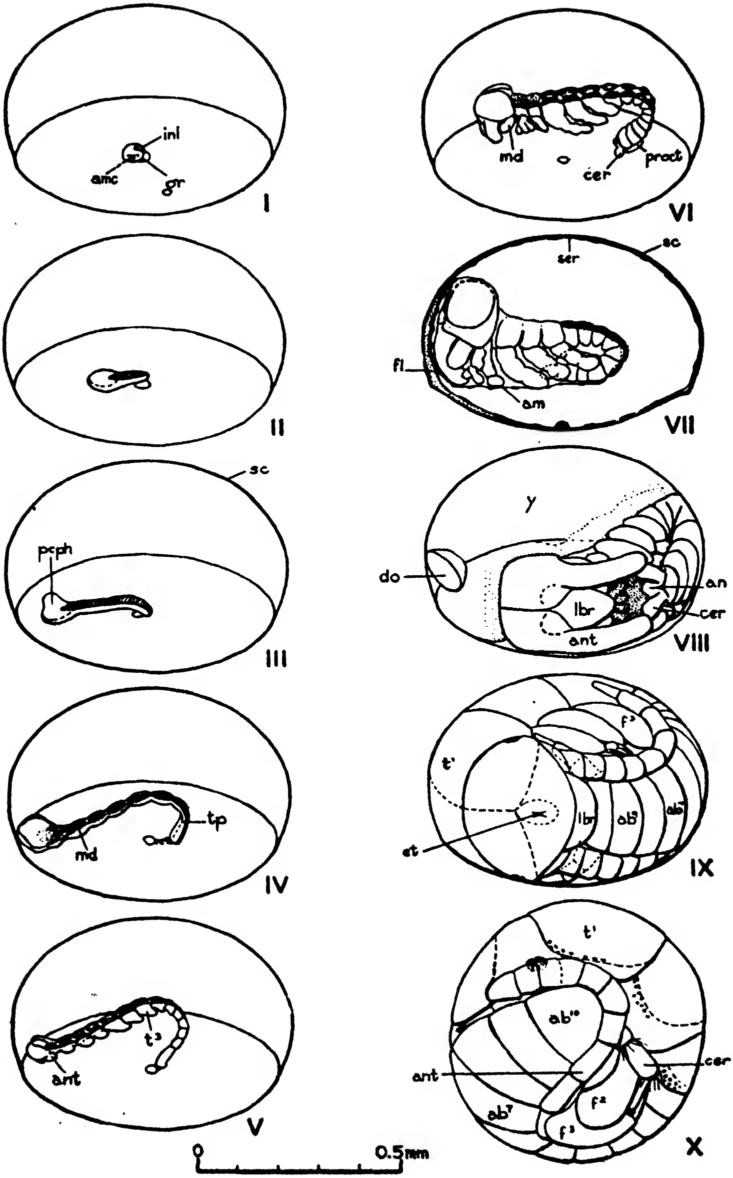

FIG. 164. Embryonic growth and segmentation in a stonefly. *ab*, abdominal segment; *am*, amnion; *amc*, amniotic cavity; *an*, anus, *ant* antenna; *cer*, cercus; *do*, dorsal organ; *et*, egg tooth; *f*, femur; *gr*, grumulus; *inl*, inner layer; *lbr*, labrum; *md*, mandible or mandibular segment; *pcph*, protocephalon (= prostomium + first postoral segment); *proct*, proctodeum; *sc*, serosal cuticle; *ser*, serosa; *t*, thoracic segment; *tp*, tail piece; *y*, yolk. (After Miller)

pendages, but most of the abdominal appendages become only poorly defined. In many groups of insects all the abdominal appendages except the cerci are never more than small rudiments which are reabsorbed at an early stage. The anterior segments and appendages develop more rapidly than the posterior ones, so that as a rule the embryo at this stage appears as in fig 166.

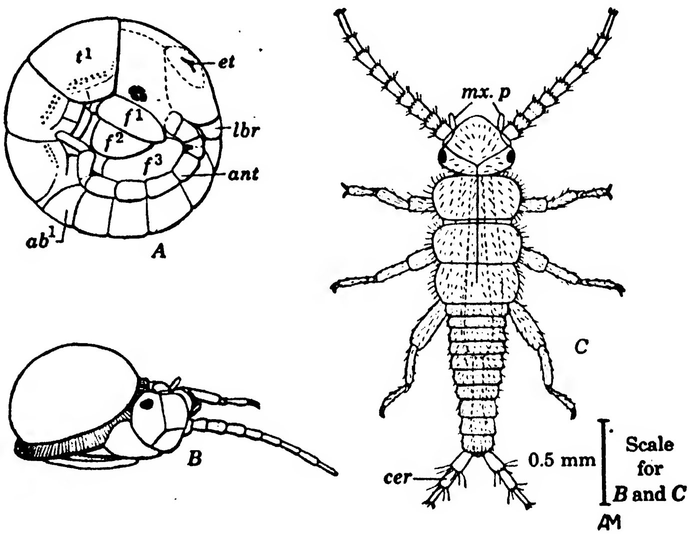

FIG. 165. End of embryological development in the stonefly. *A*, embryo in egg; *B*, completed embryo escaping from egg shell; *C*, newly hatched nymph. Abbreviations as for fig. 164. (After Miller)

Body Shape. In the early stages only the appendages and the ventral portion of the body are formed. Thus, in fig. 164, V and VI, there are no sides or dorsum, the embryo representing the appendages and the sternal region. In essence, the body is open on top. During later growth the sides grow out and up, first anterior and posterior extremes. Figure 164, VIII, shows a stage when the head is closed dorsally and also the posterior four or five segments of the abdomen; the embryo rests so that the open "top" of the intervening segments is pressed against the yolk, which fills the rest of the egg. From this stage the lateral margins of the open segments grow out and up along the sides of the egg until they meet dorsally, inclosing the yolk and completing the body closure.

Germ Layers and Gastrulation. At first the germ band consists of only a single layer of cells, but early in embryonic life it forms a second layer. This is usually formed by gastrulation, that is, the infolding of a section of the germ band. In insects the common method by which this is achieved is shown diagrammatically in fig. 167. Gastrulation begins as a central longitudinal groove of the germ band,

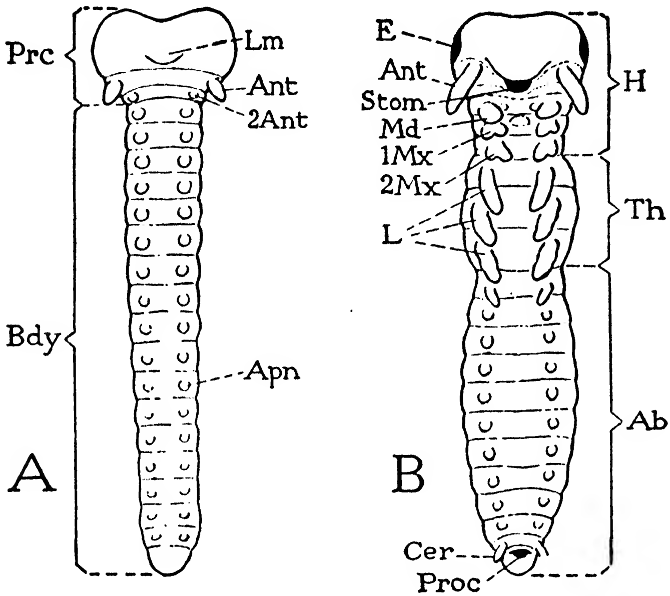

FIG. 166. Embryo at early stages of appendage development. *A*, early embryo consisting of embryonic head, or procephalon (*Prc*), formed of three segments, and of a body (*Bdy*) with as many as 18 segments, each but the last with a pair of ventral appendages (*Apn*). *B*, a later stage, showing segment grouping of adult insect; head (*H*) of six segments; thorax (*Th*) of three segments; abdomen (*Ab*) of at most 12 segments. *Ab*, abdomen; *Ant*, antenna; 2 *Ant*, rudimentary second antenna; *Bdy*, body; *Cer*, cercus; *E*, compound eye; *H*, head, of adult composition; *L*, legs; *Lm*, labrum; *Md*, mandible; 1 *Mx*, first maxilla; 2 *Mx*, second maxilla or labium; *Prc*, primitive embryonic head, or procephalon; *Proc*, opening of proctodeum (the anus); *Stom*, opening of stomodeum (the mouth); *Th*, thorax. (After Snodgrass)

A; the outside edges of the groove grow toward each other, and the future second layer proliferates inward, *B;* finally the edges of the groove meet and fuse to form an outer layer or ectoderm. The inner layer or mesoderm spreads out above it, *C*. In fig. 164, I to V, the mesoderm is shown as a darkened dorsal area.

The ectoderm gives rise to the body wall, the stomodeum and proctodeum of the digestive tract, the nervous system, tracheal system, the heart, and many glands. The mesoderm gives rise to the mesenteron, the muscular system, the gonads, and the fat body.

Embryonic Coverings. During much of its development, the embryo becomes partially or entirely immersed in the yolk, presumably for protection, and a pair of membranes form around it. The two princi-

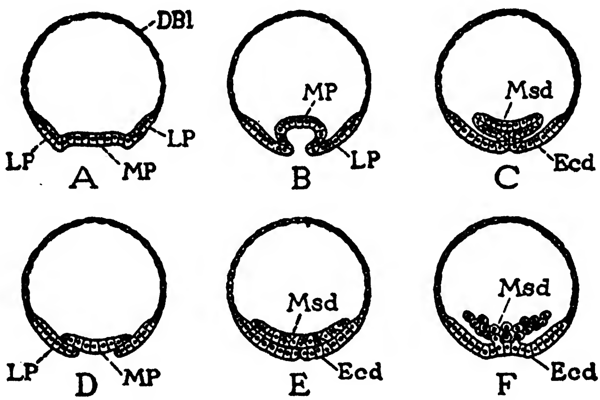

FIG. 167. Development of mesoderm by simple gastrulation methods. *A,* cross section of egg with germ band differentiated into lateral plates (*LP*) and middle plate (*MP*). *B,* later stage of same with middle plate curved in to form a tubular groove, edges of lateral plates coming together below it. *C,* still later stage, with edges of lateral plates united, forming the ectoderm (*Ect*), and middle plate spread out above the latter as internal layer of cells, the mesoderm (*Msd*). *D, E,* second method of mesoderm formation: middle plate, separated from edges of lateral plates, becomes mesoderm (*Msd*) when lateral plates unite beneath it. *F,* third method, in which mesoderm (*Msd*) is formed of cells given off from inner ends of middle plate cells. (After Snodgrass)

pal methods followed are illustrated in fig. 168. In the first, the embryo slides tail first into the yolk, pulling the membrane with it, fig. 168*D*. When the embryo is completely immersed, fig. 168*E*, the membrane grows over the end of the entrance cavity to form two final membranes; the outer one is the *serosa,* and the inner one (which incloses a space around the ventral aspect of the embryo) is the *amnion.* The second method by which immersion occurs involves only a sinking of the embryo into the yolk, fig. 168*G* to *I;* the membrane grows over the ventral area, and the opposing membrane edges unite to form the amnion and serosa. At a later stage of development the embryo changes position again, breaking through the two membranes and assuming a position with its back to the yolk, as in fig. 168*F*.

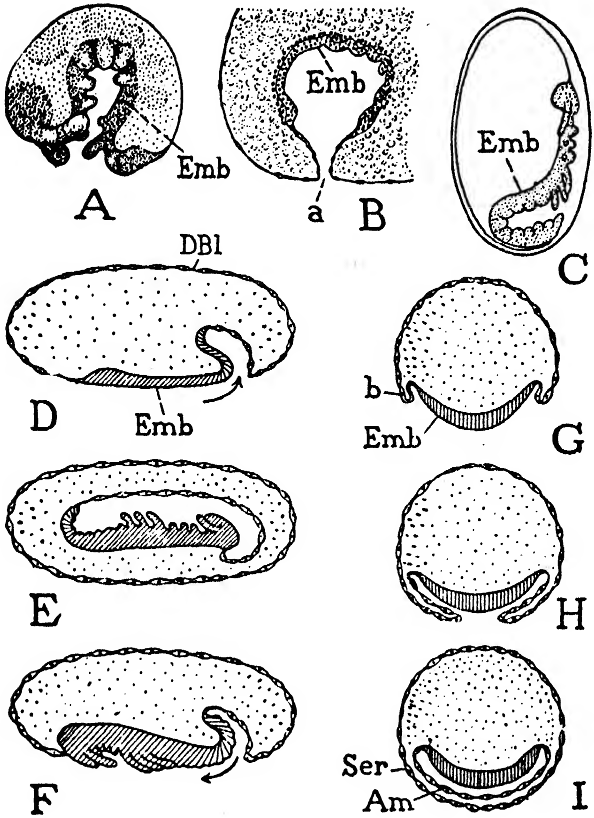

FIG. 168. Diagrams of position and movement of embryo within the egg, illustrating three methods. *A*, *embryo* (*Emb*) of a springtail *Isotoma cinerea*, curved into the yolk on under side of egg.

B, C, embryo of a silverfish *Lepisma:* first (*B*), at early stage when deeply sunken into yolk near posterior end of egg, the opening of the cavity closed to a small pore (*a*); and second (*C*), in later stage when partially revolved to outside of egg, in which position it completes its development.

D–F, lengthwise sections of an egg in which the embryo revolves rear end first into the yolk (*D*), becoming entirely shut in the latter (*E*) in reversed and inverted position, and then again revolves to surface (*F*) in original position before hatching.

G–I, cross sections of an egg in which embryo becomes covered by membranes originating in folds of the blastoderm around its edges (*G, b*), the folds extending beneath the embryo (*H*), and finally uniting to form two membranes (*I*), the outer serosa (*Ser*), the inner the amnion (*Am*). (From Snodgrass, *A* after Philiptschenko; *B* after Heymons)

Formation of Digestive System. A detailed discussion of the origin and formation of the various insect organs is beyond the scope of this book. The formation of the digestive tract, however, is of unusual interest, and a brief outline of its early growth is illustrative of the general fashion in which organs arise. The successive stages in the formation of the digestive tract are shown diagrammatically in fig. 169. In fig. 169*A* there are two masses of mesoderm cells, the anterior mesenteron rudiment *AMR,* and the posterior mesenteron rudiment *PMR,* growing inward from each end of the embryo. In fig. 169*B*

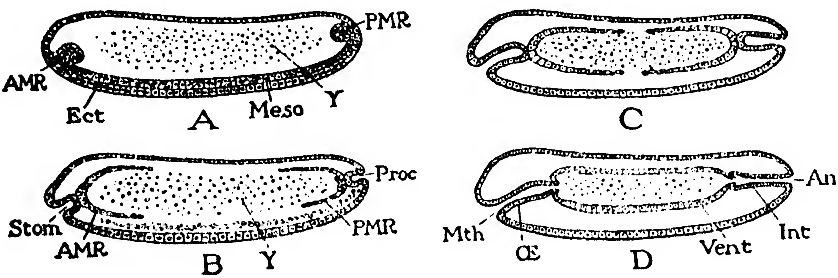

Fig. 169. Embryonic formation of the alimentary canal. *AMR,* anterior mesenteron rudiment; *An,* anus; *Ect,* ectoderm; *Int,* hind intestine; *Meso,* mesoderm; *Mth,* mouth; *OE,* oesophagus; *PMR,* posterior mesenteron rudiment; *Proc,* proctodeum; *Stom,* stomadeum; *Vent,* mesenteron; *Y,* yolk. (After Snodgrass)

each of these rudiments has begun the formation of a sac, open toward the middle of the body, and beginning to inclose the central yolk mass; at the same time the ectoderm at each end has invaginated to form the beginnings of the anterior and posterior parts of the digestive tract. In fig. 169*C* these developments have continued to a further stage. The completed structure is shown in fig. 169*D;* the anterior and posterior sacs of the mesenteron have joined, completely inclosing the remains of the yolk; and openings have formed connecting the mesenteron with the anterior and posterior ectodermal invaginations. The digestive tract thus has three distinctive areas: (1) The anterior stomodeum, formed of ectoderm; (2) the central mesenteron, of mesodermal origin; and (3) the posterior proctodeum, of ectodermal origin.

Hatching. When the embryo is full grown and ready to leave the egg, or hatch, it must force its way through the eggshell or chorion by its own efforts. Prior to hatching, the embryo may swallow air or the amniotic egg fluid to attain greater bulk or turgidity. In the actual hatching process, the embryo uses rhythmic muscular activity to press against the anterior part of the shell, or to strike it repeatedly with its head.

In some insects, such as the grasshoppers, the embryo simply forces a rent in the anterior part of the eggshell. In others, such as many Hemiptera and certain stoneflies, fig. 165*B*, a portion of the egg forms an easily detached cap, which the embryo pushes open like a lid. In a third group, the anterior part of the embryo is armed with an egg burster, which may be a sclerotized saw, spine, or some blades which pierce the chorion to produce the initial tear.

Once the shell is broken, the embryo works its way out of the egg. In many cases the nymph is encased in an embryonic covering or pronymphal membrane which is molted when the nymph is partway out of the egg. The cast skin remains inside or protruding from the egg. The egg burster is a thickening of this pronymphal membrane. When free from the egg and its embryonic coverings, the embryo is considered as the first-stage nymph or larva of the postembryonic period, fig. 165*C*.

Polyembryony. The eggs of certain parasitic Hymenoptera frequently produce more than one embryo. In *Platygaster hiemalis*, a parasite

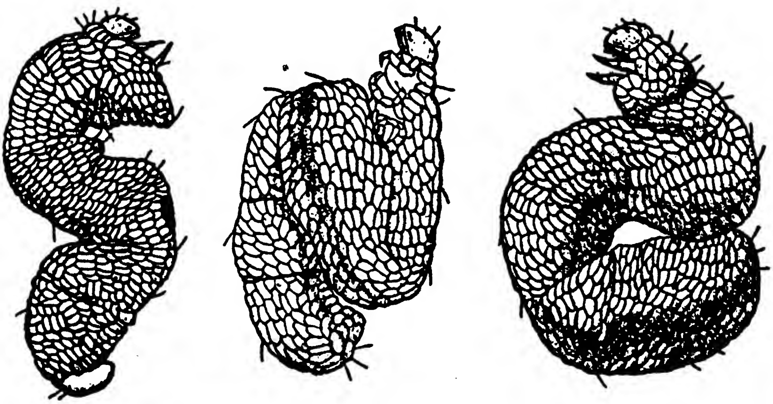

FIG. 170. Polyembryony in the chalcid *Litomastix;* the 2000 parasite larvae in this host caterpillar all developed from one egg. (From Clausen, after Sylvestri, "Entomophagous Insects," by permission of McGraw-Hill Book Co.)

of the hessian fly, each egg may develop two embryos; in *Macrocentrus gifuensis*, a member of the Braconidae, each egg may develop several embryos; and in other species each egg may produce one hundred to three thousand embryos. Each of these embryos develops into an active larva. The division into multiple embryos takes place before any other embryonic development occurs. The segmentation nucleus divides by mitosis into the required number of daughter nuclei, and each of these then develops into an embryo. The embryos may form either irregular groups or long chains. By means of polyembryony, a small parasite can insert a single egg into a large host and by that one egg produce enough offspring to take advantage of the great food possibilities of the host. An example of this is the minute chalcid, *Litomastix truncatellus,* which parasitizes large Lepidoptera larvae, fig. 170; from only a small number of eggs over two thousand larvae usually develop in caterpillars, and these allow no part of the host to go to waste.

Postembryonic Development; Metamorphosis

From the time of hatching from the egg to adulthood the individual passes through a period of growth and change. The insect integument has no stretch, and so to accommodate increase in size the insect periodically sheds its old skin and replaces it with a larger one. The mechanics and physiology of molting are discussed on page 122. Most insects molt at least three or four times, and in some cases thirty or more molts occur during normal development. The average is five or six molts.

The process of molting is sometimes called *ecdysis.* The old skins cast off by the insect are called *exuviae.*

Instar and Stadium. With few exceptions the molts for each species follow a definite sequence as to number, duration of time between them, and the increase in size accompanying them. The total period between any two molts is called a *stadium.* The actual insect during a stadium is termed an *instar.* Thus from time of hatching until the first molt is the first stadium. Any individual which is in this period of development is called the first instar. To put it another way, we might say of a species that the first stadium is 5 days and that the first instar is slender and yellow. In all but a few primitive wingless orders, no further molts occur after the functional adult stage is reached.

Adulthood. The *adult,* or *imago,* is the stage having fully developed and functional reproductive organs and associated mating or egg-laying structures. In winged species it is the stage bearing functional wings. The only known exception to this latter is the mayfly order, Ephemeroptera, in which the stage before the winged reproductive also has wings and uses them; this curious flying preadult instar is called a *subimago.*

Metamorphosis. In most insects there is a marked difference between the first instar and the adult. The process of change which occurs between these stages is called metamorphosis. This change embodies increase in size; development of reproductive organs and parts accessory to them; in most groups the development of wings; and frequently changes in form, appearance, and the structure of various parts of the body and appendages.

The types of metamorphosis displayed by insects can be divided into three principal categories:

A. Ametabolous—slight or imperceptible metamorphosis; wings never developed.

B. Hemimetabolous—gradual or incomplete metamorphosis; having external development of wings.

C. Holometabolous—complex or complete metamorphosis; having internal development of wings until pupal stage.

Ametabolous Metamorphosis. In a few wingless insect groups the young are practically identical with the adults except in size and reproductive ability. So little change occurs in them during their growth that they are considered as having no metamorphosis. This group is called the *Ametabola,* and among its members are the springtails (Collembola) and the bristletails (Thysanura). In most Ametabola the adult stage is not clearly delimited; reproduction is acquired before the individual reaches its maximum size, and molting continues after the individual is sexually functional.

All other insects have a definite metamorphosis and are called the *Metabola.*

Hemimetabolous Metamorphosis; Gradual or Incomplete. In this kind of metamorphosis, fig. 171, the immature instars are usually similar to the adults in general appearance of body, antennae, and legs, and also in feeding habits. The immature forms differ from the adults in lacking wings and well-developed reproductive structures.

The morphological characteristics of the adult are acquired gradually. Thus, fig. 171, each successive instar is a little more like the adult. In this type of metamorphosis the preadult instars are called *nymphs.* In the winged species wings become visible as padlike projections of the mesonotum and metanotum in the last two or three nymphal instars. In wingless species the nymphs are remarkably like the adults, and the last-instar nymphs can be distinguished from adults chiefly by the incompletely formed genitalia. The orders having this type of metamorphosis are termed the *Hemimetabola*.

In most of the Hemimetabola the nymphs feed in the same manner and on the same food as the adults. In the case of both the chewing and sucking body lice (Mallophaga and Anoplura) all instars of the nymphs are found on the host, feeding side by side with the adult in-

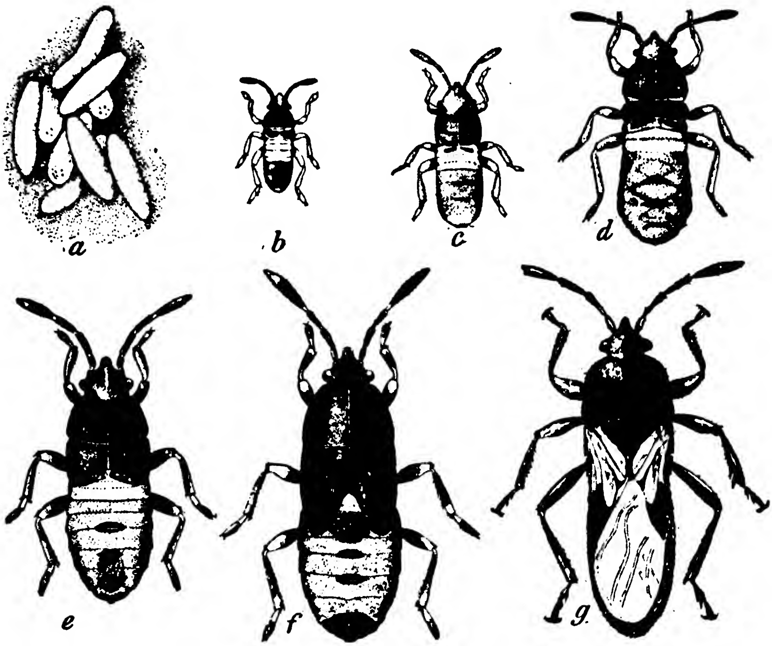

FIG. 171. Gradual metamorphosis; instars of a hemipteron, the chinch bug. (From U.S.D.A., B.E.P.Q.)

sects. Both young and adult cockroaches feed together as scavengers. In plant-feeding forms such as chinch bugs and grasshoppers, the nymphs feed on the same plant species as do the adults; in aphids and mealybugs the adults and their progeny form compact colonies on the same plant.

In three orders of the Hemimetabola the nymphs are aquatic and the adults terrestrial. In these three orders the nymphs are called *naiads* by some writers. In one of these orders, the Plecoptera or stoneflies, the metamorphosis is as simple as in the cockroaches, to which incidentally the stoneflies are closely related. The nymphs have only minor structural adaptations for aquatic life; the most conspicuous are gills possessed by some species, and vestiges of these are carried over into the adult stage. The other two aquatic orders of the Hemimetabola are the Ephemeroptera or mayflies and the Odonata or dragonflies. In these the nymphs have well-developed lateral or anal gills and other structures that are not carried over to the adult and in general are totally unlike the adults in general appearance. In these orders, however, the wings develop externally as wing pads, and there is no quiescent pupal period, so that they are true Hemimetabola.

Holometabolous Metamorphosis, Complex or Indirect. In this type the wings are developed internally until the preadult instar, in

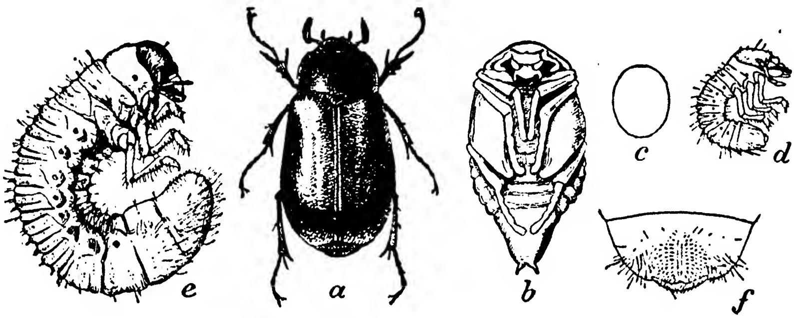

FIG. 172. Complex metamorphosis; life stages of a beetle. *a*, beetle; *b*, pupa; *c*, egg; *d*, newly hatched larva; *e*, mature larva; *f*, anal segment of same from below. (From U.S.D.A., B.E.P.Q.)

which stage the wings are everted as large pads. There are three distinct growth forms during the postembryonic period, the larva or feeding stage, the pupa or resting stage, and the adult, fig. 172.

The larva is primarily a feeding and growing stage; it is quite different in appearance from the adult, having no external wings, and frequently having small or aborted antennae and eyes. Many larvae have a feature not found in adults—functional legs, or larvapods, on the abdomen. Larvae of most Lepidoptera (moths) have five pairs, fig. 173*B*; some Hymenoptera (sawflies) may have eight pairs; and larvae of Trichoptera and a few other small groups have one pair, situated on the last segment, fig. 173*A*. The larval stage comprises few to many instars, depending on the group.

Although holometabolous larvae do not have external wing pads as do the hemimetabolous nymphs, nevertheless, wing development is fundamentally the same in both groups. In the Holometabola the wings develop as *internal* pads or pouches, known as imaginal buds or histoblasts; these are everted when the larva transforms to a pupa and are then external wing pads. In legless larvae the adult legs are formed as histoblasts in the same manner as the wings.

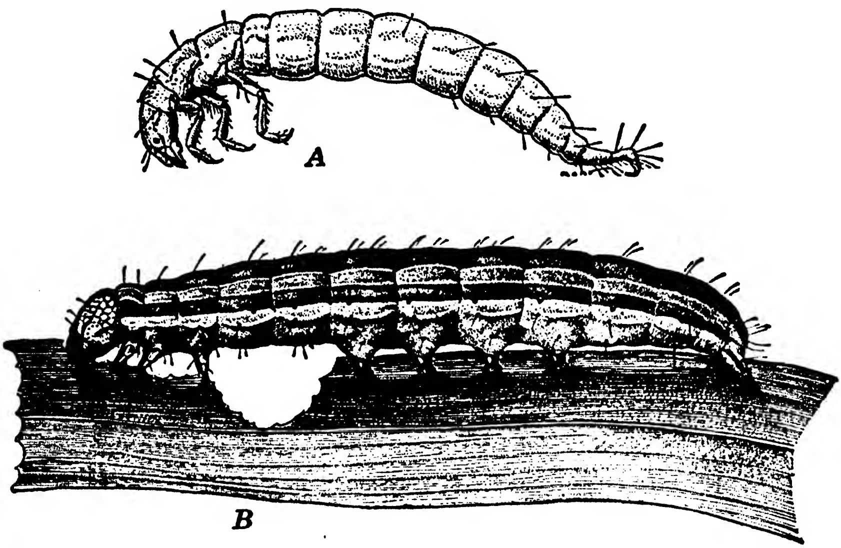

Fig. 173. Larvae having functional abdominal legs. *A*, caddisfly larva; *B*, lepidopterous caterpillar. (*A*, from Illinois Natural History Survey; *B*, from U.S.D.A., B.E.P.Q.)

Histoblasts begin to develop early in larval life, sometimes even in the late embryo. Typical stages in the growth of a wing histoblast are illustrated in fig. 174*A–G;* these are diagrammatic. At first a

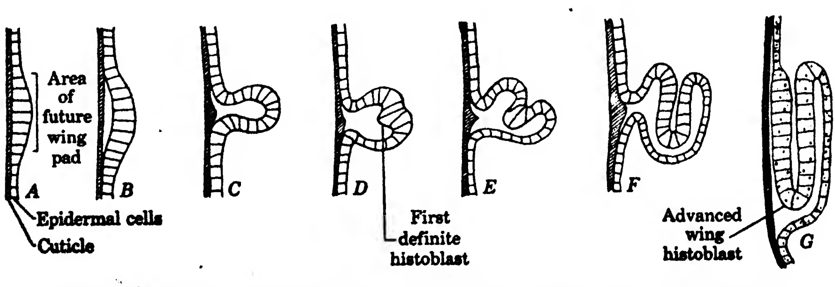

Fig. 174.—Stages in the growth of an internal wing pad or histoblast.

histoblast is only an area of thickened epithelial cells, *A*. This area enlarges, *B*, and begins to pull away from the cuticle, until it forms an internal pocket, as in *C*. One portion of the pocket wall then begins to enlarge into the pocket, as in *D*, gradually infolding to form a double-walled sac, as in *E* and *F*. Just before pupation this sac, the rudimentary wing, is usually pushed out, and the cavity flattens out, so that the sac lies directly underneath the cuticle, as in *G*. When the cuticle is shed during the molt to the pupal instar, the wing is finally an exposed external structure. If rudimentary wings are dissected out of the histoblasts, they look very much like wing pads of hemimetabolous nymphs.

The *pupa* is a non-feeding quiescent stage; the body and appendages are usually shaped somewhat as in the adult but have a less definite outline. In Coleoptera, Hymenoptera, and some other orders the pupa is soft and flabby, with the appendages held loosely at the side of the body, fig. 172*B*. In the Lepidoptera the pupa is heavily sclerotized, and the appendages are held closely and rigidly against the body, figs. 348 to 350; in some groups the appendages are "countersunk" in grooves and appear to be fused solidly with the body.

The pupa is frequently housed in a cocoon spun by the larva before pupation. Often the larva forms a cell in the ground, and pupation occurs there. In many families of Diptera (flies) the pupal stage is passed inside the last larval skin. After the pupa is formed, the inclosing larval skin hardens into an impervious protective shell called a *puparium*, fig. 380.

The pupal stage is one of transformation. The tissues are reorganized or developed to bring about the change from larva to adult. The mechanism of these changes is outlined on page 142, Physiology.

The *adult* is the final instar possessing fully developed reproductive organs and, in most species, wings. The primary function of the adult is reproduction. So highly developed has this become in some species, that the adult stage is short-lived and takes little or no food. In other groups, especially the Coleoptera (beetles), the adult is long-lived and eats almost as much as the larva.

In the Coleoptera it is usual for the adults to have the same type of mouthparts as the larvae and to feed on the same food or same general kind of food. For instance, both adults and larvae of the fungus beetles feed on fungi, and both stages may be found feeding side by side. In the case of the leaf beetles belonging to the genus *Diabrotica*, the subterranean larvae are herbivorous, feeding on the roots of plants; the adults are also herbivorous, feeding on the leaves of plants, although not always the same plant species as that attacked by the larvae.

The adults of many holometabolous orders have mouthparts of a different type from those found in their larvae and have entirely different food habits. This is especially true in the Diptera. Mosquito

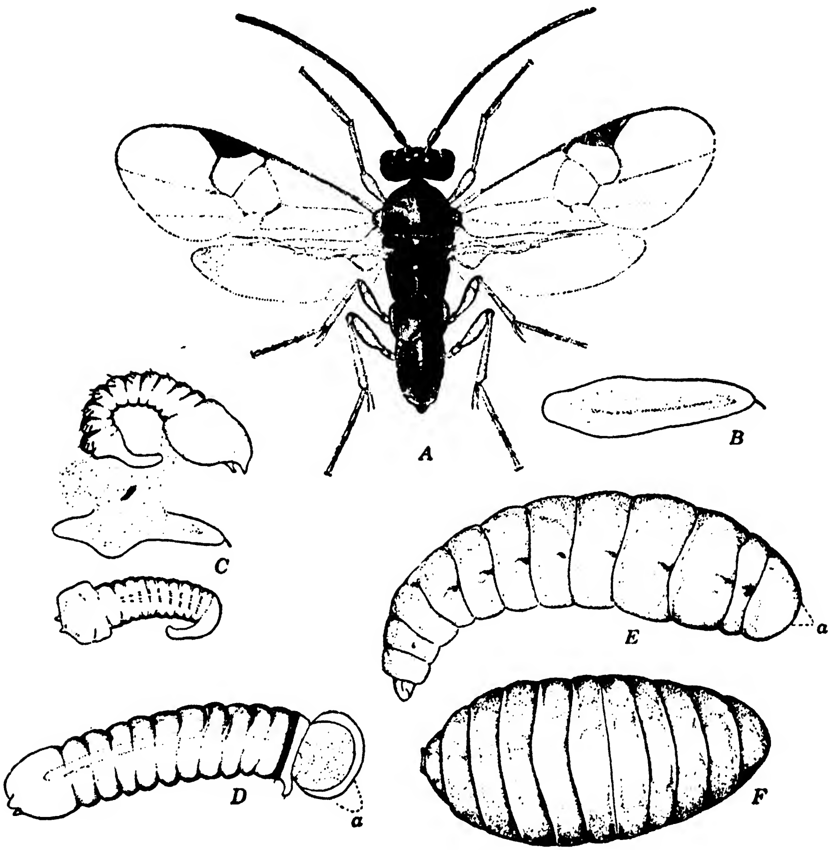

FIG. 175. Stages of the life cycle of a parasitic hymenopteron, *Apanteles melanoscelus*. *A*, adult; *B*, egg; *C*, first-instar larvae, the upper one with yolk still attached to it; *D*, second-instar larva; *E*, third-instar larva in feeding stage; *F*, same, but ready to spin cocoon (prepupal stage). *A*, anal segment. (From U.S.D.A., B.E.P.Q.)

larvae, which are aquatic, have chewing mouthparts, and most of them feed on microorganisms; the adults have piercing–sucking mouthparts, the males feeding on nectar and most of the females on avian or mammalian blood. The order Siphonaptera (fleas) offers another striking example. Flea larvae feed as scavengers on inert organic material, and the adults suck blood.

Hypermetamorphosis.* In the majority of the Holometabola all the larval instars of a species are similar in feeding habits and general appearance, differing chiefly in size. Some groups of Holometabola however, may have two or more quite distinct types of larvae in the life cycle. When this occurs, it is called hypermetamorphosis. Among the best examples are many of the parasitic Hymenoptera, fig. 175. The first-instar larva is a motile form bearing bristles, tails, or other processes; this instar either penetrates the host integument or migrates through host tissues. The later instars are sedentary and have none of the modifications of the first instar. Another striking example is the suborder Strepsiptera (illustrated on p. 365). The young larvae are active legged forms furnished with bristles and tails; the succeeding instars are grubs. The same sort of development occurs in the blister beetles Meloidae, fig. 307, although in these the difference between larval instars is chiefly general shape accompanied by few structural changes.

Transitional cases are frequent, in which various instars differ considerably in shape and habit but have few morphological differences, as is the case with more pronounced hypermetamorphic forms. For instance, certain parasitic rove beetles have slender active first-instar larvae and grublike succeeding instars. A few genera of caddisflies (Trichoptera) have free-living slender first-instar larvae and casemaking stout-bodied later instars (p. 371, fig. 332).

Pedogenesis. This is a precocious reproductive maturity which occurs in a few insects, resulting in the production of eggs or living young by larvae or pupae. In the life cycle of the rare beetle, *Micromalthus debilis,* some larvae lay eggs or produce young.. Midge larvae of the genera *Miastor* and *Oligarces* produce young but no eggs. Pupae of the midge genus *Tanytarsus* may produce either eggs or young. Pedogenesis is a freak type of metamorphosis and growth involving a maturation of the reproductive organs without a similar maturation of other adult characteristics. It often is associated with unusual generation cycles, discussed on page 204.

MATURITY

Sexual Maturity and Mating. Adult insects are seldom sexually mature immediately on emerging from the preadult stage. In most cases the males require a few days to mature, and the females longer. Mating occurs in many forms before the females have mature eggs;

the sperms are stored in the spermatheca of the female until the time for their use.

In the case of certain short-lived insects, such as many mayflies, both sexes are fully mature sexually within a matter of hours after completing the last molt. Mating takes place a day or so after emergence, and oviposition occurs shortly afterwards.

Parthenogenesis. This ability to reproduce without fertilization is possessed by certain insects. In some species parthenogenesis occurs only irregularly. In certain sawflies (Hymenoptera), unmated females lay eggs which produce only males, while the eggs of inseminated females produce either males or females. Normally no males are produced at any time in some other parthenogenetic insects. The females lay unfertilized eggs, and these produce females. The pear sawfly *Caliroa cerasi* and the rose slug *Endelomyia aethiops* are examples of permanent parthenogenesis.

Oviposition. Most insects are oviparous; that is, they lay eggs; but the various kinds of insects differ tremendously in egg-laying habits. The Phasmidae (walkingstick insects) drop their eggs singly onto the ground; butterflies glue theirs to leaves; and sawflies saw out a cavity in leaf or stem to form a recess for each egg. Eggs may be laid separately, or they may be grouped together in large masses. Extruded eggs of stoneflies and mayflies collect as a mass at the end of the body; this mass is deposited as a unit. In the cockroaches this tendency is greatly developed. The eggs are glued together as they emerge from the body and, cemented by glandular secretions, form a compact capsule or oötheca, which is deposited. In forms such as the mayflies, oviposition is completed with the deposition of a single large mass of eggs. Oviposition in bedbugs occurs at a slower rate but continues for a period of months. These are only a few examples; additional material is incorporated in the synopsis of the orders in the following chapter.

Viviparity. Not all insects lay eggs. Species of various groups are viviparous; that is, they deposit living young instead of eggs. In viviparous insects the eggs develop in the oviducts or vagina until at least the completion of embryonic growth. This phenomenon occurs in many groups scattered throughout the insect orders. There are several kinds of viviparity in adults, some cases being only slight modifications of the oviparous condition and others involving the development of special structures.

Precocious hatching of the embryo within the egg passage occurs in the flesh flies, Sarcophagidae. Eggs remain in the vagina until mature and hatch just as they are deposited. The young larvae pass through the ovipositor like eggs and at birth are in an early stage of larval development, corresponding to the point of hatching from the egg in

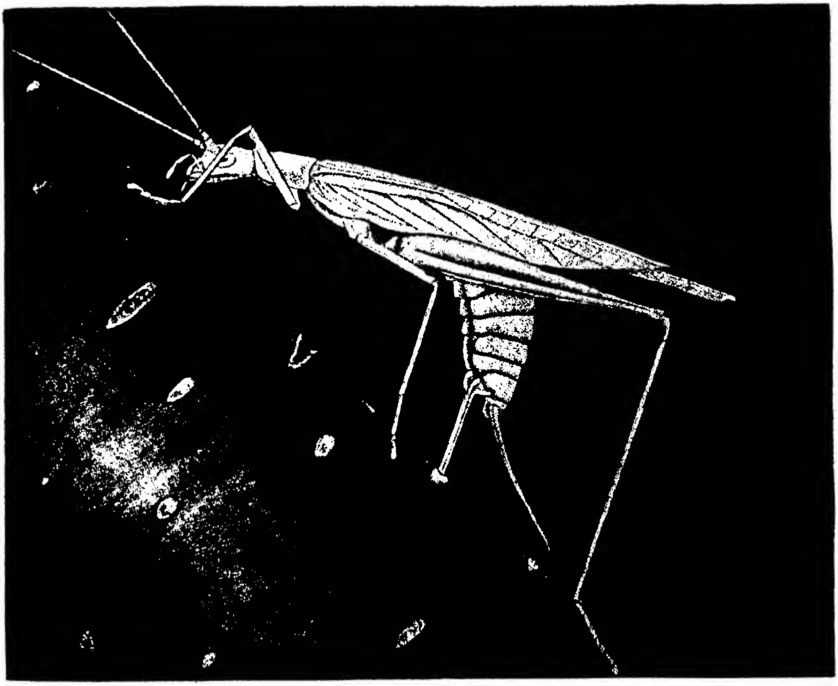

FIG. 176. Egg laying of the snowy tree cricket. (From Metcalf and Flint, "Destructive and Useful Insects," by permission of McGraw-Hill Book Co.)

oviparous species. In Strepsiptera (Coleoptera) the eggs hatch inside the body of the female and the minute larvae crawl out through the genital openings.

Vaginal development of larvae occurs in the ked flies, Pupipara, and the African fly genus *Glossina* (both members of the Diptera). In these the vagina is a large chamber, fig. 177, provided with glands to produce nourishment for the larvae, which develop to maturity in the body of the female. The maggots pupate as soon as they are discharged from the vagina.

One of the more common examples of viviparity occurs in the parthenogenetic generations of aphids. The unfertilized embryos develop within the ovaries and are liberated as active nymphs equivalent to first-instar nymphs of oviparous generations.

Longevity of Adults. Adult insects have a normal life span ranging from a few days to several years, depending on the species. The length of life is correlated with fecundity, death usually occurring a short time after the completion of mating or oviposition activities. Thus the females of certain species of psocids (Corrodentia) have an adult life of about 20 days and die 5 or 6 days after final oviposition. Un-

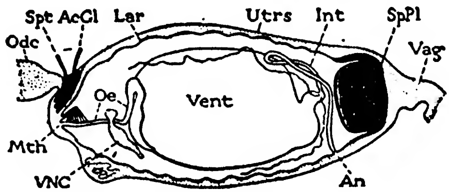

FIG. 177. Larva of the tsetse fly *Glossina,* in uterus of the parent. *AcGl,* accessory gland; *An,* anus; *Int,* intestine; *Lar,* larva; *Mth,* mouth; *Odc,* oviductus communis; *Oe,* oesophagus; *SpPl,* spiracular plate of larva; *Spt,* spermatheca; *Utrs,* uterus; *Vag,* vagina; *Vent,* ventriculus; *VNC,* ventral nerve cord. (After Snodgrass)

mated females of these species rarely oviposit and live about 20 days longer than mated females which lay the normal number of eggs. The hibernating forms in many species are adults, and in these cases they may have a life span of nearly a year. Many adult leaf beetles, for instance, mature in July, feed for the rest of the summer, and then hibernate. They become active the following spring, mate, lay their eggs through May and June, and die soon after.

FOOD HABITS

Food is essential to the growth of any organism and therefore is an important consideration in the life cycle of an insect. A wide range of organic substances, living and dead, are used by insects as food. According to the type of food utilized, insects may be grouped in the following manner with an example given for each category.

1. *Saprophagous*—feeding on dead organic matter.
   General scavengers—Blattaria (cockroaches).
   Humus feeders—Collembola (springtails).
   Dung feeders, coprophagous—some Scarabeidae (dung beetles).
   Restricted to dead plant tissue—Isoptera (termites).

Restricted to dead animal tissue—Dermestidae (larder beetles).
Carrion feeders—Calliphoridae (flesh flies).

2. *Phytophagous*—feeding on living plants.
   Leaf feeders—Saltatoria (grasshoppers).
   Leaf miners—Agromyzidae (flies).
   Stem and root borers—Cerambycidae (beetles, round-headed borers).
   Root feeders—some Scarabeidae (beetles, white grubs).
   Gall makers—Cynipidae (gall wasps).
   Juice suckers—Leafhoppers and aphids.
   Mycetophagous, fungus feeders—Mycetophagidae (fungus beetles).
3. *Zoophagous*—feeding on living animals.
   Parasites (living on another animal).
      Living on warm-blooded vertebrates—Anoplura (sucking lice).
      Living on other insects—Ichneumonidae (ichneumon flies).
   Predators (seeking out and killing prey)—Reduviidae (assassin bugs).
   Blood feeders—Culicidae (mosquitoes).
   Entomophagous—either parasites or predators on other insects.

Of these food categories, two involve relations between insect and host which are quite unusual and merit further discussion. These are the gall makers and the parasites.

Gall Makers. Many insects cause plants to develop abnormal outgrowths or disfigurements called galls, fig. 178, and live within the shelter of these structures. Insect galls are formed by abnormal growth of particular tissues of a plant and may occur on leaves, buds, stems, or roots. Each insect produces a particular type of gall and always on the same region of the plant. The sawfly *Euura salicisnodus* always makes a gall on the stems of willow, and another sawfly *Euura hoppingi* always makes a gall on the leaves of willow. In certain insects that have alternation of generations, each generation may cause the formation of a differently shaped gall.

The cause of gall formation is not known exactly, but a gall is presumably excessive growth of the plant tissue brought about by either irritation caused by the presence of the insect, or hormones or growth-stimulating substances secreted by the insect. When sucking insects cause a gall, such secretions may be injected with saliva when the insect feeds. When chewing insects are involved, the secretions may be freed on the lacerated tissue of the plant and absorbed by it.

Galls are of two types, open and closed, fig. 179. Open galls are essentially pouchlike and have an opening to the outside. Aphids cause galls of this type. A gall begins to form around the feeding station of a single aphid. The plant tissue around this area enlarges and gradually becomes twisted or bowed to form a purselike cavity

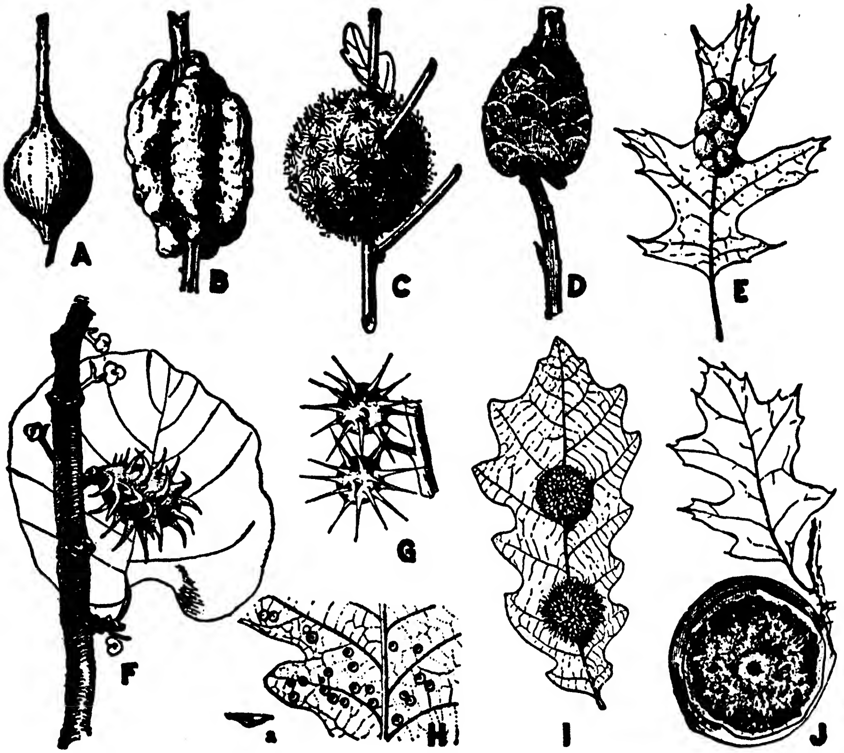

FIG. 178. Examples of insect galls. *A,* goldenrod ball gall, caused by a fly *Eurosta solidaginis; B,* blackberry knot gall, caused by a gall wasp *Diastrophus nebulosus; C,* wool sower gall on oak twig, caused by a gall wasp *Andricus seminator; D,* pine-cone gall, common on willow, caused by a gall fly *Rhabdophaga strobiloides; E,* oak leaf galls, caused by a gall wasp *Dryophanta lanata; F,* spiny witch hazel gall, caused by an aphid *Hamamelistes spinosus; G,* spiny rose gall, caused by a gall wasp *Rhodites bicolor; H,* oak spangles, caused by a gall fly *Cecidomyia poculum,* one gall shown in section at *a; I,* spiny oak gall, caused by a gall wasp *Philonix prinoides; J,* large oak apple, caused by a gall wasp *Amphibolips confluens.* (From Metcalf and Flint, rearranged from Felt)

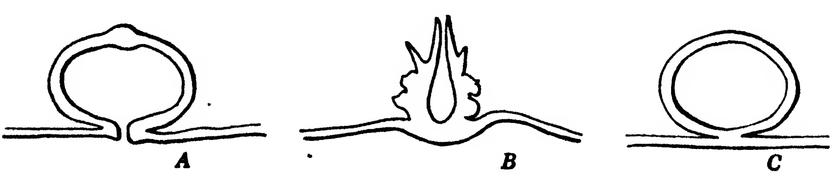

FIG. 179. Diagram of open and closed galls. *A* and *B,* open galls; *C,* closed gall. (*A* and *B* redrawn from Wellhouse)

with the aphid inside. The edges of these galls are usually tightly appressed until a generation of aphids within have completed their growth; at this point the edges separate and allow the migrating aphids to escape from the gall. The galls of *Phylloxera* and mites are also of this type.

Closed galls are formed by several groups of Hymenoptera, including a few genera of sawflies, certain groups of Chalcid flies, and the family Cynipidae. In these groups the females insert each egg beneath the surface into the plant tissue. The larva never leaves this haven, feeding on the inner tissues of the gall which forms around it. The insect must eat its way out. In some sawflies the larva leaves the gall and pupates elsewhere; in others the larva pupates within the gall, and the adult eats its way out.

Parasites. In the zoological sense, a parasite is an animal that lives in or on another animal, known as its *host,* from which the parasite derives its food for at least some stage in its life history. Several insect groups are true parasites. On the basis of habits and hosts, insect parasites fall into two categories—parasites of warm-blooded vertebrates, and parasites of insects or other small invertebrates such as spiders and worms.

The insects parasitizing warm-blooded vertebrates do not kill their host, so that many individuals or many generations of the parasite may live on the same host animal. Sucking lice (Anoplura) and chewing lice (Mallophaga) are examples of external parasites. They spend all their lives on a bird or mammal host, frequently occurring in large numbers on the same animal, and having continuous generations during the life span of the host. Seldom does the host die from these attacks, although its general health and resistance to other maladies may be greatly impaired. Bot flies and warble flies furnish excellent examples of internal parasites. The larvae of these flies live and mature in the nasal passages, stomach, or back of the host, and when full grown leave the host and pupate in the soil. Many individuals of the parasites may infest one host individual. Again the host is not killed, although harmed, and is attacked by successive generations of the parasites.

Insects which parasitize other insects differ from those parasitizing vertebrates in two particulars: (1) Usually only a single parasite attacks a host individual, and (2) the parasite usually kills the host. As with the internal parasites of vertebrates, only the larvae actually live entirely on the host. This type of parasitism occurs in many families of Hymenoptera, several families of Diptera, and a few genera of Coleoptera.

Parasites of insects usually infest a host in one of three ways. The most common manner is for the female to lay an egg on the host or to insert her ovipositor through the host integument and lay an egg in the host tissue. Most of the parasitic Hymenoptera and Diptera use this method. The second manner is an indirect approach. The parasitic female deposits her eggs on leaves of the plant on which the insect host feeds. If the host eats some of the egg-infested leaves, the parasite eggs are unharmed and hatch within the digestive tract, the larvae making their way into the host tissue. The hymenopterous family Trigonalidae and many species of the Tachinidae, or tachina flies, use this method. In the third manner the eggs are laid more or less in random places, and the first larval instar finds it way to a host, as in the Meloidae (p. 352) and Stylopidae (p. 364).

Most of these parasites are internal, but in a number of parasitic Hymenoptera the larvae feed externally on the body of the host. In these instances the circumstances approach closely the condition of predatism rather than parasitism.

The habit of parasitism is an extremely specialized one. Thousands of species of Hymenoptera and Diptera are parasitic; yet each species usually parasitizes only a single host species or a group of closely related species. The parasites, called primary parasites, are often the host to other parasites, called secondary parasites, and these may be the host to tertiary parasites. Usually secondary and tertiary parasites are much less specific in host selection than are primary parasites.

Feeding and Life-Cycle Stages. In general, the life of the adult insect is concerned primarily with reproduction. The adult feeds to maintain its metabolic losses due to activity and life processes, or to furnish nutriment to the eggs or sperms developing in its body. In such groups as Orthoptera, Hemiptera, Siphonaptera, and blood-sucking members of the Diptera, the adult requires a large amount of food to supplement the reservoir from nymphal or larval stage.

In many groups sufficient stores of fats or other nutrients are carried over from the immature stages to the adults that these latter need to do little or no feeding. This is true of caddisflies (Trichoptera), many Hymenoptera, Lepidoptera, and Diptera. In extreme cases such as the mayflies (Ephemerida), the eggs are practically ready to deposit by the time the adult emerges, and no feeding is done in this stage. This last example is an extreme in the direction of non-feeding on the part of adults, and there are also extremes in the opposite direction. The most outstanding instance in our fauna is the sheeptick group, Pupipara (Diptera). In these the larvae develop to maturity in the body of the female, and she does all the active feeding in the life cycle. A somewhat parallel situation is found in the bees and many wasps, which gather food for the larvae.

SEASONAL CYCLES

Whereas the *life cycle* is the development of the individual from egg to egg, the *seasonal cycle* is the total successive life cycles or generations normally occurring in any one species throughout the year, from winter to winter.

The life cycle of many species consists of a single generation each year. In this case the life cycle and seasonal cycle are the same.

In cases such as the housefly there are continuous generations produced throughout the warmer months, followed by a hibernating period or diapause (see p. 143). Thus the seasonal cycle consists of several life cycles.

There are some species in which the life cycle is longer than a year in duration, as, for instance, many June beetles, whose larvae require 2 or 3 years to mature, and the 17-year locust, a cicada having a 17-year developmental period. In these insects the seasonal cycle includes only a portion of the life cycle. In most cases, however, the generations overlap so that adults of each species are produced every year; the seasonal cycle is used here to include the activities of the combined generations of the species for the year.

Seasonal cycles made up of more than one life cycle are of two types, those having repetitious life cycles, and those having alternation of generations.

Repetitious Generations

In this category successive life cycles are fundamentally the same. One generation of houseflies, for instance, lays eggs which develop into another generation just like the first, having the same morphological characteristics, food habits, and reproductive habits.

Interruptions in the development of certain generations, due to estivation, hibernation, or other types of diapause, are not considered as altering fundamentally the general pattern of the life cycle. To cite the housefly again, it has successive generations during the summer, the life cycle of each varying from 4 to 5 weeks, depending on weather conditions; adults produced in autumn, however, hibernate during the winter and in spring resume normal activities. A life cycle interrupted by onset of winter differs from that of summer in no feature other than the time element.

Alternation of Generations

There are several groups of insects in which succeeding generations are quite different in method of reproduction and sometimes in habits.

Forms with Reproduction Only by Adults. Two well-known groups belong in this category, the aphids and the gall wasps. These forms are all plant feeders.

The aphids (Aphididae, Hemiptera) have varied and complicated seasonal cycles involving sexual oviparous and parthenogenetic viviparous generations, winged and wingless generations, and frequently migrations between definite and different summer and winter host plants. A fairly simple seasonal cycle is exemplified by the cabbage aphid, *Brevicoryne brassicae.* Members of this species overwinter as eggs, laid in autumn on the stems of cruciferous plants. These hatch the following spring and develop into the wingless parthenogenetic viviparous form, the stem mothers. It is interesting to note that all the eggs develop into these stem mothers. These produce parthenogenetic viviparous generations which may be winged or wingless. Similar viviparous generations are continuous throughout the summer. As a rule parthenogenetic individuals live about a month and produce 50 to 100 young. When the days become shorter in autumn, the viviparous forms produce the sexual generation, wingless females and winged males. After mating, each female lays one to several eggs, which pass through the winter.

More complicated seasonal cycles have several additional specializations. Many species migrate to summer hosts. In these the winter or primary host is usually a tree or shrub. The eggs are laid on such hosts in autumn, hatch in spring, and develop into wingless stem mothers. These normally produce winged viviparous females which fly to summer or secondary hosts. Continuous viviparous generations, either winged or wingless, are produced on these hosts until autumn. At that time migratory forms are produced which fly to the winter host and there produce young of the sexual generation. In certain species the winged males are produced on the summer host, migrate to the winter host, and mate with the wingless oviparous females. In other species both males and females are wingless, in which case they are both produced by winged viviparous females which have previously migrated to the winter host.

Season	Non-Migratory Species	Typical Migratory Species	
	All forms on one host	Forms on primary host	Forms on secondary host
Winter	Eggs	Eggs	
Early spring	Stem mothers Apterous viviparous females	Stem mothers Apterous viviparous females	
Late spring	Alate viviparous females (spring migrants)	Alate viviparous females (spring migrants)	Spring migrants from primary host.
Summer	Alate and apterous viviparous females (these migrate from plant to plant of the same host species, or compatible related species)	A few strays	Alate and apterous viviparous females
Early fall		Fall migrants from secondary hosts.	Alate viviparous females, sometimes alate males (fall migrants)
Late fall	Sexual forms: males and oviparous females	Sexual forms: males and oviparous females	
Winter	Eggs	Eggs	

Fig. 180. Chart of alternation of generations in aphids, illustrating a form with no host alternation, such as the cabbage aphid; and one having an alternation of hosts, such as the plum aphid.

There are radical differences in habits among various generations of some aphids. In the genus *Pemphigus,* for example, the stem mother makes a gall on the leaf or petiole of poplar; her progeny migrate to the roots of Compositae and other plants and initiate a series of root-inhabiting generations.

The phylloxerans (Phylloxeridae, Hemiptera), closely related to the aphids, also have an alternation of parthenogenetic and sexual

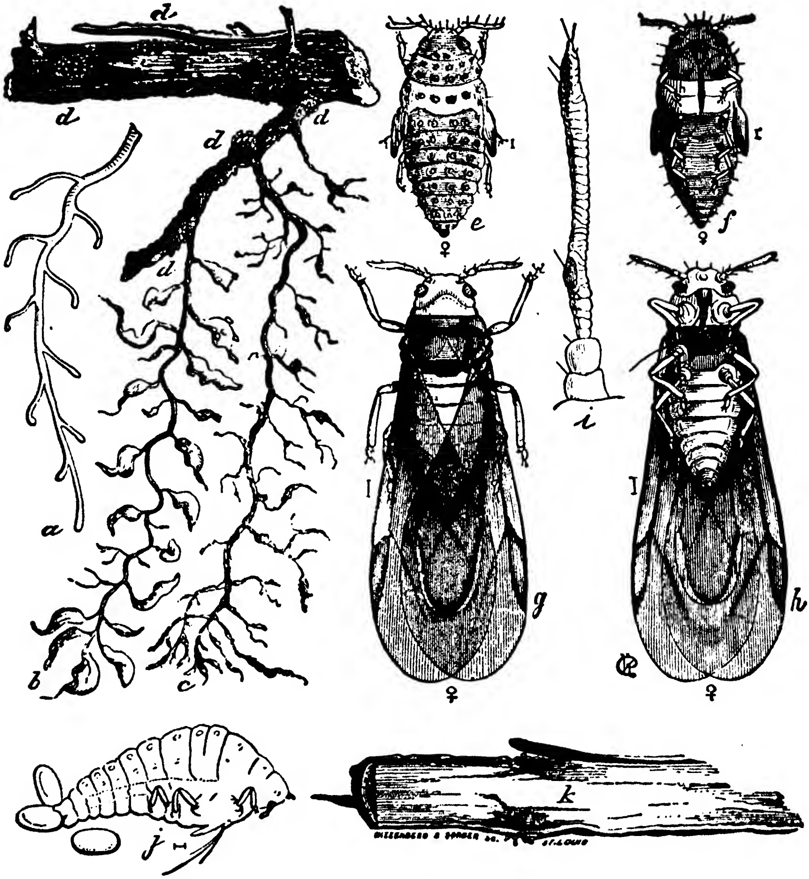

FIG. 181. Root-inhabiting form of the grape phylloxera. *a,* shows a healthy root; *b,* one on which the insects are working, representing the knots and swellings caused by their punctures; *c,* a root that has been deserted by them, and where the rootlets have commenced to decay; *d, d, d,* show how the insects are found on the larger roots; *e,* agamic female nymph, dorsal view; *f,* the same, ventral view; *g,* winged agamic female, dorsal view; *h,* same, ventral view; *i,* magnified antenna of winged insect; *j,* side view of the wingless agamic female, laying eggs on roots; *k,* shows how the punctures of the insects cause the large roots to rot. (From Riley)

generations (some winged and others wingless) and complicated migration habits. They differ from aphids, however, in that all forms are oviparous. A common example is the grape phylloxera, fig. 181. A series of parthenogenetic generations form leaf galls, migrating in autumn to the grape roots, where the following spring another series of parthenogenetic generations form enlargements and galls on the small grape roots. Some of the root forms give rise to parthenogenetic winged migrants in the autumn; these crawl out of the ground and fly to the grapevines, there producing wingless males and females. After mating, the females each lay one egg in a crevice of the bark. The eggs overwinter and hatch the next spring, initiating a series of leaf-infesting generations.

The gall wasps (Cynipidae, Hymenoptera) contain many species having alternation of sexual and parthenogenetic generations. An example is an oak-feeding species *Andricus erinacei* which overwinters as eggs laid in leaf or flower buds. These hatch in spring, and each larva becomes surrounded by a soft bud gall produced by the plant. The inner layer of the galls provides food for the larvae. In early summer, when those larvae mature, winged males and females emerge. The females lay their eggs in the veins of oak leaves. Larva from these eggs cause pincushion-like growths on the leaf veins, called hedgehog galls. Larvae in the hedgehog galls mature in autumn, and all emerge as short-winged females, which reproduce parthenogenetically, laying the overwintering eggs in the oak buds.

The benefits of alternation of generations are undoubtedly concerned with food supply. The habit allows the species to feed on more species of hosts, or more individuals, or on different parts of the same host. This in turn permits larger populations of the insect species to be produced without danger of the food supplies being curtailed.

Forms with Pedogenesis. Pedogenesis involving reproduction by larvae is always combined with a complex and irregular cycle of generations. The cases studied indicate that there may be successive generations of pedogenetic larvae, with irregular production of larvae which mature normally and pupate. Adults from these pupae mate normally and produce fertilized eggs. The beetle *Micromalthus debilis* has a complex cycle of pedogenetic and normal generations. The most completely studied examples are in the midge family Cecidomyiidae, especially the European *Oligarces paradoxus*. For this species a typical cycle of generations, shown diagrammatically in fig. 182, is as follows: A pedogenetic larva *a* produces larvae *b* which may grow up to be one of four types: (1) another pedogenetic larva like *a*, or (2) a female-producing larva *c*, or (3) a pedogenetic larva *d* which gives birth only to male-producing larvae *e*, or (4) a pedogenetic larva *f* which gives birth to both male-producing larvae *e* and other pedogenetic larvae like *a*. The male- and female-producing larvae pupate, and normal adults emerge. The females lay fertilized eggs which develop into the pedogenetic larvae *a*.

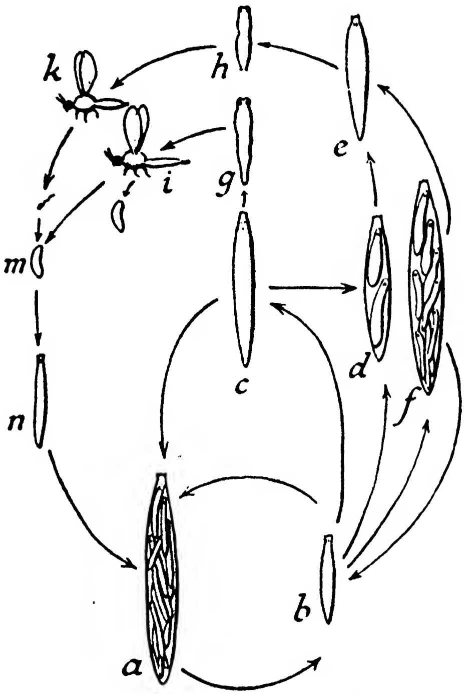

FIG. 182. Succession of generations in the midge *Oligarces paradoxus*. *a*, paedogenetic larva giving rise to *b*, undetermined daughter larva which may develop into *a* again or into *c*, female-imago-producing larva, or into *d*, which gives rise to male-imago-producing larvae (*e*) or into *f*, which gives rise both to undetermined daughter larvae and to male-imago-producing larvae; *g*, female pupa; *h*, male pupa; *i*, female imago; *k*, male imago; *l*, sperm; *m*, egg; *n*, young larva from egg. (From Wigglesworth, after Ulrich)

In *Oligarces paradoxus* adults are produced more frequently as the colony becomes overcrowded or the food supply less ample. In the pedogenetic species of the midge genus *Miastor*, temperature changes have a determining effect on the type of generation produced. Thus in these midges the cycles of pedogenetic generations are correlated with day-to-day conditions as well as a more inclusive seasonal cycle.

SOCIAL INSECTS

In mode of life the great majority of insects are solitary. Each individual lives to itself, and members of a species have no marked attraction for each other except at times of mating. Beyond placing the eggs or young on or near their food, the parents usually take no interest in their offspring. The parents usually die before their progeny matures, and consequently there is no opportunity for prolonged parent–offspring relationship. There are certain groups of insects, however, whose species have a social mode of life. In the termites, ants, social wasps, and social bees social life is well developed and complex, embracing almost all phases of the individual's activities. Other insects show interesting tendencies toward the beginnings of social life, through such phenomena as maternal care, social larvae, and community development.

Maternal Care. The females of certain earwig species deposit their masses of eggs in a sheltered chamber and guard them, driving away

Fig. 183. Maternal care exhibited by female earwig. (After Fulton)

predators. After the eggs hatch, this watch is continued for a short time until the young nymphs are active enough to leave the brood chamber. At this point maternal care is discontinued, and each nymph goes its own way. Similar observations have been recorded for a few other insects, among them the mole crickets *Gryllotalpa*.

FIG. 184. Communal home or tent of tent caterpillar. (After U.S.D.A., B.E.P.Q.)

Social Larvae. Among the moths (Lepidoptera) are species in which the larvae, hatching from the same egg mass together, construct a silken weblike nest, and all use it as a common abode. The nest is built around a fork or branch of a tree, all the larvae contributing to its construction. The larvae leave the nest during the day to feed on the foliage of the tree, and all return to it for resting. Larvae of the tent caterpillars (*Malacosoma*) live in the nest for their entire larval period, leaving it finally to pupate. Larvae of fall webworms (*Hyphantria*) spin a similar nest but leave it and follow solitary existences for the last larval instar.

Community Development. In the order Embioptera or web spinners, some species are gregarious. They live in colonies that consist of interlocking silken tunnels in soil, surface cover, or the base of plants. The females exercise maternal care to a high degree, watching over the eggs and young nymphs. Some of these colonies are described as forming a solid silken mat over many square yards of ground and must contain hundreds and possibly thousands of individuals. To date, however, no intimate relationship has been observed among individuals of a colony, and therefore the gregarious nature of the forms may mean little more in a social sense than the clustering of aphids or scale insects on or about their parents and grandparents.

From the standpoint of development toward social life, a more significant type of colony occurs in the cockroaches. Wood cockroaches of the genus *Cryptocercus* live together as family colonies in rotten logs. The cockroaches eat wood, which is digested by a specialized symbiotic protozoan fauna in their digestive tracts. When young cockroaches molt, they completely empty the digestive tract, so that after molting they have no symbiotic fauna, and the nymphs would soon starve if this situation were not remedied. The newly molted nymphs replenish their supply of Protozoa by eating some of the fresh excrement of another member of the colony. This necessary interchange of Protozoa requires that groups of individuals live together in a colony.

Social Life. The ants, termites, certain wasps, and a few kinds of bees have developed social life to a high level. They live in family colonies that have a division of labor among individuals and an interchange or sharing of food and other things among members of the colony. In each of the four groups where it occurs, social life arose independently. This is one of the most striking known examples of parallel evolution in animal habits. The actual details of metamorphosis, feeding habits, and colony formation are different in the four social groups, often radically so; yet the final organization attained in each is remarkably similar. Because of the differences among them, it is illuminating to present a brief sketch of the social features of the four groups.

Termites (the order Isoptera) form a definite colony, either hollowed out of wood or built from masticated products, and populated by several different forms. At certain times of the year swarms of winged sexual forms issue from the old colonies and disperse. After their flight, these forms alight, and the wings fall off. Males and females pair off and together begin a small excavation for a new nest. At this stage mating occurs, and later the female deposits and watches over her first brood of eggs. She feeds the first young with saliva

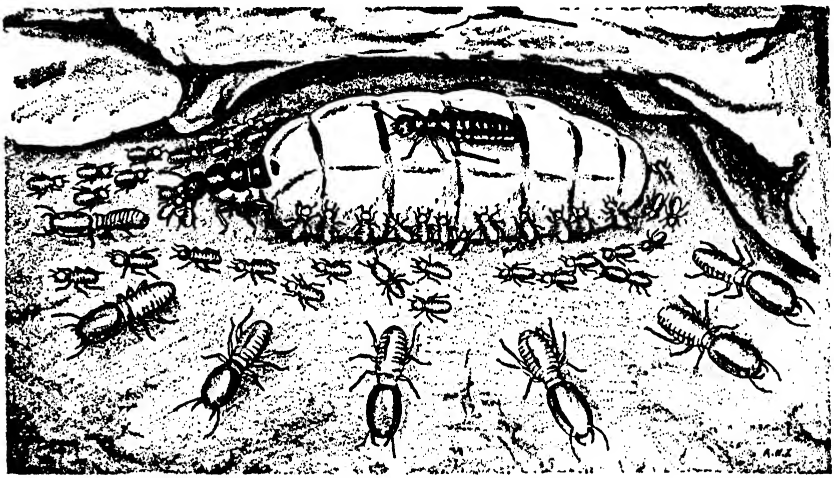

FIG. 185. A nest of termites, diagrammatic. The greatly enlarged queen rests in her royal cell with the king on her abdomen. Surrounding the queen are numerous workers grooming and feeding her. Guarding the workers are the soldiers with their greatly enlarged heads, while, among the workers, smaller soldiers (traffic police) regulate the movement of the workers. (From Matheson, "Entomology for Introductory Courses," by permission of Comstock Publishing Co.)

and other secretions. Thus a new colony is founded. Soon after hatching, the nymphs are self-reliant and feed themselves and their parents also. From this time on the original male and female, called the royal pair, perform only the function of reproduction. In the early stages of the colony, the nymphs develop into three castes, fig. 185, all of them wingless: (1) a worker caste, which is simple in structure, feeds on wood or fungus products, and by regurgitation feeds the young and other castes; (2) a soldier caste that is large-headed and has a protective function in the colony, guarding the nest entrances and the royal pair; and (3) a substitute reproductive caste that may become fertile and replace the royal pair if the latter die. There are usually two kinds of substitute reproductives, one with well-developed wing pads (but never wings), called second-form queens, and one without wing pads and very similar to the worker caste, called third-form queens. The non-reproductive castes contain both males and females, but their reproductive organs are vestigial. In some species the soldiers may be replaced by a long-headed form having a long snout. This caste, called nasutes, fig. 221, emits a disagreeable odor that is apparently designed to keep away enemies. After the colony is flourishing, periodic broods of winged reproductives are produced which disperse to found new colonies.

Nearctic termite species nest in cavities hollowed out in the ground or in wood. Some neotropical species build elaborate nests in trees, and certain species in Africa and Australia build mounds on top of the ground. The mounds of a particular species have a distinctive shape and size and range in height from a few inches to 20 feet, fig. 186. These nests or houses are built by the workers, using a "plaster" of saliva and earth or wood masticated together. It is remarkable that these structures are so uniform in shape and size, made as they are by thousands of workers who never see the nest from the outside. The instinctive behavior pattern responsible for this and other activities is one of the most amazing phenomena displayed by animals.

Among the various members of the colony there is a constant exchange of materials. Workers give food to soldiers and reproductives and in return obtain from them secretions from mouth or anus. The queens are thought to secrete desirable substances at many points on the body, because other castes lick her body as well as obtaining oral or anal secretions from her. This exchange of substances is called *trophyllaxis*.

Termites, like the wood cockroaches, have in their intestines a symbiotic protozoan fauna which predigests cellulose eaten by the termites. Without these symbionts the termites would be unable to subsist on their wood or mycelium diet. The Protozoa are passed from termite to termite by way of the secretions of which the termites are very fond. It is probable that social life in this group originated as family colonies centered around the dissemination of symbionts, as we find them today in the wood cockroaches.

The actual mechanics by which the different castes are produced has been a subject of research and speculation by many investigators. Except for the primary sexual caste, all forms in the colony are individuals that, even when mature, fail to develop complete adult characteristics. More specifically, the mature second-form reproductives develop functional reproductive organs, but their wings never grow beyond the wing-pad stage, in this latter respect resembling the last nymphal stage of the perfect form; the mature third-form reproduc-

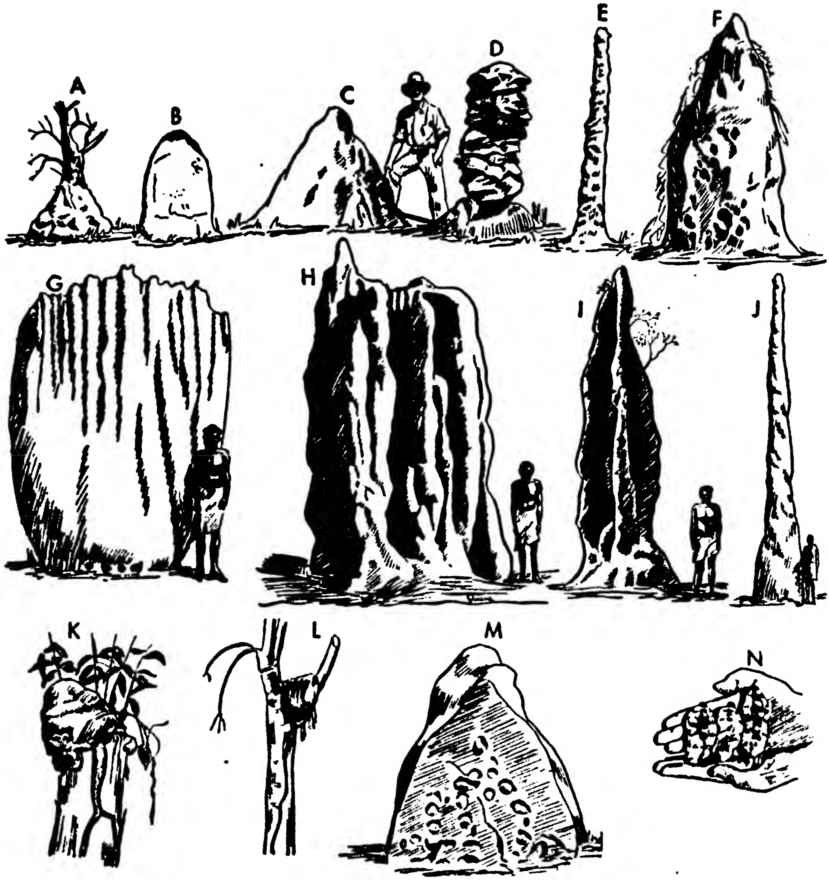

Fig. 186. Termites mounds or termitaria. *A, B, C, D, J,* from South Africa; *D, Nasutitermes lamanianus,* Belgian Congo; *E,* vent of subterranean nest, South Africa; *F* and *M,* exterior and cross section of mounds of *Termes redemanni,* Ceylon; *G, Amitermes meridionalis,* Australia; *H, Nasutitermes triodiae,* Australia; *I, Nasutitermes pyriformis,* Australia; *K* and *L,* niggerhead nests of *Nasutitermes corniger,* Panama; *N,* queens of *Macrotermes bellicosus,* Nigeria. (From Essig, "College Entomology," by permission of The Macmillan Co.)

tives have the functional reproductive organs but lack any trace of wings, in this last character being similar to an early nymphal stage; and the workers and soldiers fail to develop either functional reproductive organs or any trace of wings.

This situation implies that a control of growth is responsible for the differences among the castes. The control is differential or qualitative and probably consists of a set of complex hormones, each of which may affect one part of the insect and yet not interfere with others. Evidence based on study of embryos indicates that certain phases of growth regulation are imposed on the individual before it hatches from the egg. But some control is exercised during the entire life of the individual. For example, the substitute reproductives do not become functional until the queen dies or is removed; then several individuals of the substitute caste begin to lay eggs. It has been suggested that in this and similar cases growth hormones are exchanged from caste to caste by trophyllaxis. Thus the functional queens may secrete a hormone that inhibits the growth of certain adult characteristics and prevents maturation of the substitute reproductives. When the queen dies, the inhibition would be removed and allow the maturation of the reproductive system of the substitute reproductives. There is a further possibility that substances eaten by the queen, offered by various castes, may contain hormones influencing the quality of eggs and young and aid in keeping fairly constant the numerical ratio of the different castes in the nest.

These speculative hypotheses are based on little in the way of experimental proof but have considerable justification in colony observations. For there is no doubt that some pliable mechanism exists that allows each colony to adjust itself to misfortunes and depredations, an adjustment which could not be made with a behavior pattern controlled completely by inflexible blind instincts.

In contrasting social life in the termites with the habits of solitary insects, it is apparent that several features of termite habits are of special significance in making possible their type of social life. These features are:

1. Care of eggs and young by parents during the founding of a colony.

2. Greatly extended life span of the sexually mature adults, over a period of several years, during which many generations of progeny are matured.

3. The feeding of parents and young by offspring of the reproductives which began the colony.

4. Control of individual growth leading to a development of different castes, correlated with a division of labor within the colony.

Ants (Formicidae, Hymenoptera) exhibit a type of social life closely paralleling that of the termites in organization. A typical ant nest, or colony, is usually in a log or cavity, or in the ground, and often has a mound of earth above it. Colonies vary in number of individuals, from a few dozen to many thousands. Each colony is founded by a migrant winged queen. After the mating flight, the males die, and the females lose their wings. When well developed, the colony contains the original queen, a large number of wingless sterile workers, frequently wingless sterile large-headed soldiers, and the

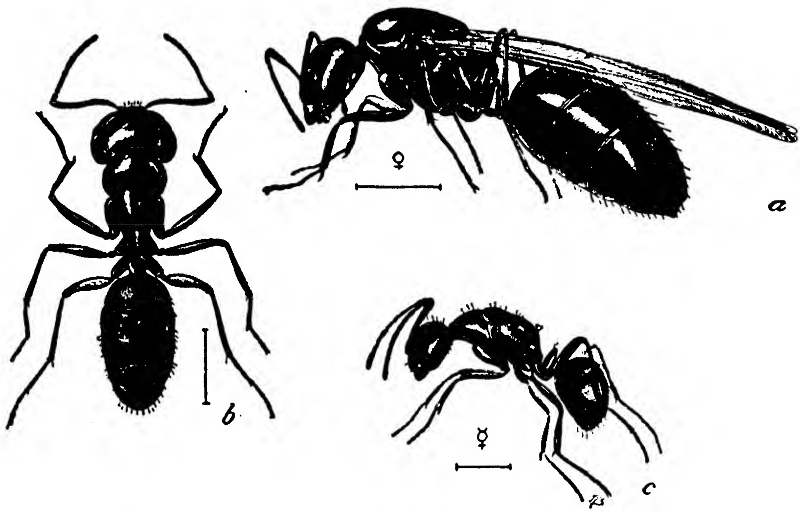

Fig. 187. Castes of the carpenter ant. *a*, winged female; *b*, large worker; *c*, small worker. (After U.S.D.A., B.E.P.Q.)

brood or young. In respect to metamorphosis ants are quite different from termites. The latter are hemimetabolous, and the nymphs are active and able to feed themselves soon after hatching. But ants are holometabolous. Their immature stages are legless helpless grubs, incapable of moving about, and they must be fed for their entire period of development. After this the larvae pupate, in some groups spinning a cocoon and in others lying naked in the nest. In the early stages of the colony, only sterile workers (or neuters) are produced, these having no wings and only vestigial reproductive organs. When the colony is well established, periodic broods of winged males and females are produced, and these disperse.

The four habit features listed for termites apply also to the ants, although with modifications regarding the manner in which each is executed: 1. The life span of only the female queen is prolonged, since one mating suffices for her life of several years, and the males die after the nuptial flight. 2. The maternal care of the first eggs and young by the queen when founding a new colony covers a more protracted period because the larvae must be nourished until they are mature. During this period the queen's wing muscles undergo histolysis to provide the source of both the queen's own nourishment and the oral secretions she feeds her first brood of larvae. 3. The workers take over feeding of the queen and brood after the nest is established. 4. There is the same control of development, with production of different castes and a division of labor.

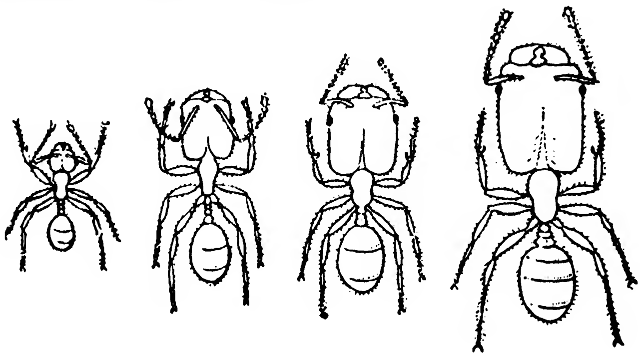

FIG. 188. Heterogony in the ant *Pheidole*. Neuters of *Pheidole instabilis* showing increase in the relative size of the head with absolute size of the body. (From Wigglesworth after Wheeler)

Ants have an exchange of foods between individuals as have termites, the workers feeding queens, soldiers, and larvae, and obtaining exudates or anal secretions from each. Ants are omnivorous and apparently have no peculiar intestinal fauna as have the termites. Trophyllaxis in the ants, therefore, seems to be a simple "reward" system by which the receiver pays the giver. The role played by the possible exchange of growth hormones in ants is unknown.

Whether an individual develops into a sexual form or a neuter is thought to be determined in the egg. Among the neuters, however, are many cases of polymorphism due to heterogony. In heterogony different parts of the body grow at different rates, so that in small individuals all parts may appear well proportioned, but in larger individuals some part or parts may appear unusually large. In the case of ants, the head is usually the region of disproportionate growth. Thus in *Pheidole*, fig. 188, small neuters have heads and abdomens about the same size; in larger individuals the head becomes disproportionately larger, and in the largest individuals the head is enormous.

The larger-headed forms perform special services such as cracking seeds or acting in a soldier capacity and are usually considered as an additional caste. The amount of food given to the larva determines the size of the neuter developing from it; hence, the workers are able to control the production of certain castes by feeding.

Social wasps, comprising *Vespa, Polistes,* and certain related genera of the Vespidae, and *social bees* of the families Bombidae and Apidae, are social in habits, living in colonies and having a caste of sterile workers. All these differ from both termites and ants in certain respects. The workers are winged and differ in appearance from the queens chiefly in their smaller size. Both wasps and bees are holometabolous insects and have legless grubs which must be fed for their entire growth period, as is the case with ants. The bees and wasps, however, construct an individual cell for each larva, and the cell is sealed during pupation. Wasps feed on insects; bees on nectar and pollen. Except for honeybees, the nearctic wasps and bees make only annual colonies. These are started each year by a fertilized female. She begins the nest, lays eggs, and forages food for the first brood of young. These mature into workers, who take over the duties of nest making and foraging for the colony. In fall only males and females are produced. These disperse, and mate, the males dying soon after mating, but the fertilized females hibernate for the winter and emerge the following spring to start new colonies. At the approach of winter old queens and workers die.

Honeybees are much more specialized socially than the other social bees. Their colonies are perennial, made possible by storing during the summer enough food to keep the colony alive through the colder months when there are no flowers to provide essential nectar and pollen. Beginnings of this storage habit are found in more specialized species of bumblebees (*Bombus*), close relatives of the honeybees. In nests of these bumblebees a few cells are constructed for storage of food, which is used later in the fall when flowers are less abundant. In a honeybee nest (normally built in a hollow tree) there are vertical rows of wax cells, or combs; a large number are used for raising the brood, but a goodly number are used for storage of food, in the form of honey. During the cold months individuals of the colony are active, though sluggish, within the nest and by oxidation of foodstuffs in their bodies keep the nest temperature well above freezing. Unfertilized honeybee eggs produce males or drones; these do no work. They stay around the nest for mating purposes but after a few weeks are driven out by the workers. Fertilized eggs develop into either queens or workers, depending on the diet given the larvae. Those fed "royal jelly" (a milky product of glands in the heads of workers) and afterwards pollen and nectar develop into workers; those fed royal jelly for their entire larval period develop into queens. Since the workers do all the feeding, they determine the production of queens.

The queens have lost the power of founding new colonies alone. This is accomplished by swarming, in which a queen and part of a worker colony leave the nest together, seek a new site, and start a new colony. In this feature the honeybee is different from all other social insects.

Social Life Cycles. Social insects differ from others in that the *colony* and not the *individual* is the reproductive unit. The productivity of the reproductive caste is made possible by the home building, foraging, and protection performed by sterile workers and soldiers. The instincts and behavior pattern which will result in new generations of these sterile castes in a new nest must be represented in the genes carried out of the nest by migrating reproductives.

We have seen how certain insect species have a cycle of dissimilar generations, each generation specialized to aid in some way the welfare of the species. In social insects we have the same principle applied, except that the various generations (reproductives, workers, and soldiers) all occur contemporaneously and work side by side in a common abode. In all four groups in which this social phenomenon occurs there is a division of labor or biological functions: One caste performs the reproductive function, a second caste the feeding function, and sometimes a third the function of protection. This is carrying to individuals the same kind of specialization that occurs in the cells of the metazoan body.

AQUATIC INSECTS

Insects are predominantly terrestrial, but certain orders, families, or genera are aquatic and spend at least some stage of their life cycle in water. Most investigators consider that ancestral insects were terrestrial, and that present-day aquatic forms represent a modification from the primitive or generalized mode of living. This is well borne out by the taxonomic composition of aquatic insects, for they comprise an aggregate of many diverse groups more closely related to various terrestrial groups than to each other. Some aquatic groups are isolated families of orders that are essentially terrestrial, such as Coleoptera (beetles). Structural evidence pointing in the same direction is found in the tracheal system, an apparatus basic to all insect groups and indubitably evolved for breathing in an aerial rather than aquatic medium.

Aquatic insects differ greatly in the portion of the life cycle spent in the water and in food habits of the aquatic stages. These are summarized in the following paragraphs:

Ephemeroptera, Odonata, and Plecoptera. All species in these orders are aquatic, and all are hemimetabolous. The eggs and nymphal stages live in the water; the adults are aerial. The Odonata (dragonflies) nymphs are predaceous; Ephemeroptera (mayflies) and Plecoptera (stoneflies) nymphs are mainly herbivorous, but each of these latter two orders have a few genera that are predaceous.

Hemiptera (Bugs). Six families are aquatic; three families, the Corixidae, Notonectidae, and Belostomidae, are rapid swimmers; the other three families, Pleidae, Nepidae, and Naucoridae, walk or crawl over objects in the water. The entire life cycle is spent in the water except for dispersal flights of the adults. The Corixidae and Pleidae feed on plant material and organic ooze; the others are predaceous. Semiaquatic members of the order are mentioned in the next subsection.

Coleoptera (Beetles). About ten families are aquatic, including the Gyrinidae, Dytiscidae, and Dryopidae. The eggs, larvae, and adults live in water; the pupae are formed on land. Some are swimmers, others are crawlers; some are predaceous, others herbivorous or scavengers. In a few other families isolated forms may have aquatic larvae and terrestrial adults, such as leaf-feeding beetles of the genus *Donacia.*

Neuroptera (Lacewings). A single small family, the Sisyridae, has aquatic larvae, which live in fresh-water sponges. The pupae and adults are terrestrial.

Megaloptera (Dobsonflies and Alderflies). All members have aquatic predaceous larvae. The pupae and adults are terrestrial, and the eggs are laid out of water.

Hymenoptera (Wasps). A few genera of minute wasps parasitize aquatic eggs of some aquatic insects. The larvae are the same as related forms that parasitize terrestrial eggs, but the adult wasps have the curious habit of entering the water, using their wings as paddles, and swimming about in search of host eggs.

Trichoptera (*Caddisflies*). All stages are aquatic except the adults, and eggs of some species which are deposited on branches overhanging water. In Europe one genus is an exception, the larvae living in moss and humus. The aquatic species include both predaceous and herbivorous species.

Lepidoptera (*Moths*). A few genera are aquatic. Both larvae and pupae live in water, and the adults are terrestrial. The larvae are herbivorous.

Diptera (*Flies*). Many families have aquatic larvae, and some have aquatic pupae also; all the adults are terrestrial, some circling over and resting on the water but never going below the surface. Common examples are the Chironomidae or midges, and the Culicidae or mosquitoes, that have both larvae and pupae aquatic. In the Tabanidae or horseflies, the larvae are aquatic, but the pupae are normally found in moist places above the water line. Aquatic Diptera deposit their eggs in water, or on objects above it, or on low ground subject to flooding. Larvae of aquatic Diptera are predators, herbivores, or scavengers.

Aquatic insects have a number of modifications for their life in water, chiefly concerning respiration and locomotion. The most diverse adaptations occur in the respiratory system and include development of areas of hairs that hold a film of air, gills, and extensile air tubes. These are discussed in the chapter on physiology (see p. 149).

For locomotion many aquatic groups have developed wide flat fringed legs for swimming. The nymphs of dragonflies eject water from rectal respiratory chambers to propel themselves through the water, an interesting form and use of jet propulsion.

Semiaquatic Insects. In the order Homoptera there are several families like the Gerridae or water striders, that live on the surface of water. These are termed semiaquatic. The group includes predators and scavengers, feeding on insects and other small organisms that either occur naturally on the surface or become stranded there. The semiaquatic individuals have hygrophobe (water-repelling) hairs on the underside of the tarsi, enabling them to walk on the surface-tension membrane with as much ease as others walk on dry surfaces. This same characteristic is found in the adults of certain aquatic Diptera, notably those Ephydridae having aquatic larvae. Some Collembola live on the surface of water and use the surface-tension membrane for support, walking and leaping on it with ease.

Marine Insects. Few insects live in the ocean. Several species of water striders and a few Chiromomidae (midges) are marine, occurring away from shore. The remaining few insects living in the ocean are found between the high- and low-tide marks, where they live submerged when the tide is in. Mosquitoes, punkies (Ceratopogonidae), and a few other aquatic insects live in salt marshes and brackish water near estuaries, but not in the open sea.

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7

The Orders of Insects

In North America there are about eighty thousand different kinds of insects. In order to associate together related forms and to furnish a practical means of identification, these species are grouped into a system of orders, families, and genera. The North American insect fauna represents twenty-eight orders, over five hundred families, and many thousand genera.

The characters most useful for identifying insects to order are: (1) wings, their development, texture, venation, and number; (2) mouthparts, whether of the chewing, sucking, or other modified type; and (3) the kind of life history and immature stages.

The class Insecta is divided into three subclasses: the Myrientomata, including only the order Protura; the Oligoentoma, including only the order Collembola; and the Euentoma, containing all the other insects.

Key to Orders of Common Insects

1. Wings well developed, fig. 194, the front pair sometimes forming hard wing covers, fig. 290 2
   Wings reduced to minute pads, or no wings developed 24
2. Front wings hard, horny, opaque, and veinless, in repose folding over the body and forming wing covers, fig. 290 3
   Front wings either transparent, membranous, or with definite veins 5
3. Mouthparts forming a needle-like piercing beak, fig. 235; venation usually indicated but indistinct .... **Hemiptera,** p. 276
   Mouthparts with mandibles, fitted for chewing, fig. 291 4
4. Abdomen terminating in a pair of external forceps-like appendages, fig. 216 .... **Dermaptera,** p. 252
   Abdomen either without terminal appendages, or these pointed and stylelike, figs. 291, 297 .... **Coleoptera,** p. 333

5. Having only one pair of wings, the hind pair at most forming small, clubbed, balancing organs, or halteres, fig. 360 6
   Having two pairs of wings, although the hind pair may be small 10
6. Wings leathery or parchment-like 7
   Wings membranous, sometimes dark in color 8
7. Mouthparts forming a piercing-sucking beak, fig. 235 . . . . . **Hemiptera,** p. 276
   Mouthparts fitted for chewing, with generalized parts, as in fig. 215 **Orthoptera,** p. 239
8. Abdomen without terminal filaments; hind wings represented by halteres **Diptera,** p. 396
   Abdomen with two or three terminal filaments, as in fig. 194 9
9. Halteres present; terminal appendages short, antennae long, fig. 260 (males of Coccidae) . . . . . **Hemiptera,** p. 276
   Halteres not developed; terminal appendages very long, antennae short, as in fig. 194 . . . . . **Ephemeroptera,** p. 230
10. Front wings, and usually also hind wings, clothed with overlapping scales, fig. 333, except for window-like areas, fig. 343 . . . . . **Lepidoptera,** p. 372
    Wings bearing only scattered scales, having chiefly fine hair, bristles, or no vestiture 11
11. Tarsus ending in a round bladder-like structure, without evident claws, fig. 229 **Thysanoptera,** p. 270
    Tarsus without a terminal bladder, sometimes having large pads and/or distinct claws, fig. 235 12
12. Mouthparts forming slender stylets fitted together for piercing and sucking, and housed in a beak that is either triangular or rodlike, fig. 235 **Hemiptera,** p. 276
    Mouthparts not forming a beak, either vestigial or of the chewing or lapping type; mandibles not forming slender stylets 13
13. Abdomen having two or three terminal filaments as long as the body, and head having short hairlike antennae, fig. 194 . . . . . **Ephemeroptera,** p. 230
    Either abdomen having short terminal filaments or none, or antennae long and slender, fig. 218 14
14. Front wings leathery, hind wings membranous, the front ones when folded forming a protective covering over the hind pair, fig. 206 **Orthoptera,** p. 239
    Both pairs of wings of about the same texture 15
15. Both front and hind wings having many veins and many crossveins, forming a close network over part of the wing surface, figs. 220, 264 16
    Wings either with crossveins few in number, fig. 91, or longitudinal veins reduced, fig. 272, or both 21
16. Front and hind wing each with radius and its branches sclerotized and forming a heavy anterior band, remainder of venation semimembranous or subatrophied, fig. 220 . . . . . **Isoptera,** p. 257
    Venation sclerotized throughout 17
17. Antennae short and setalike, 5- to 8-segmented; wings long and exceedingly reticulate, fig. 197 . . . . . **Odonata,** p. 233
    Antennae elongate, usually with more than 20 segments; wings various, fig. 218 18
18. Tarsus 2- or 3-segmented . . . . . **Plecoptera,** p. 255
    Tarsus 5-segmented 19

19. Head prolonged into a trunklike beak at the end of which are typical chewing mouthparts, fig. 267 .... **Mecoptera,** p. 311
 Head not prolonged into a beak 20
20. Pronotum large, its length greater than half its width; front legs not stouter than the others, fig. 265 .... **Megaloptera,** p. 308
 Either pronotum less than half as long as wide, fig. 264, or front legs enlarged and raptorial, fig. 263 .... **Neuroptera,** p. 305
21. Tarsus 2- or 3-segmented 22
 Tarsus 5-segmented 23
22. Pronotum minute; either short wide species, less than 4 mm. long, or stout species up to 8 mm., with the mesonotum produced high above pronotum, fig. 224 .... **Corrodentia,** p. 265
 Pronotum large, flat, and nearly quadrate, fig. 218; either form slender or over-all length 10 mm. or more .... **Plecoptera,** p. 255
23. Mandibles sclerotized and large; wings clothed with minute setae, the venation either greatly reduced or forming a series of irregular cells, fig. 272 **Hymenoptera,** p. 312
 Mandibles difficult to detect, subatrophied; either small species (less than 6 mm.) with extremely hairy wings, or venation composed of regularly branching veins, fig. 91 .... **Trichoptera,** p. 367
24. Abdomen ending in two or three long "tails," fig. 192 25
 Abdomen without long terminal tails 26
25. Having three terminal tails, fig. 192 .... **Thysanura,** p. 226
 Having two terminal tails .... **Diplura,** p. 228
26. Abdomen ending in a pair of strong sclerotized pincer-like jaws or forceps, fig. 193 27
 Abdomen without stout terminal forceps 28
27. Tarsi 1-segmented; head without eyes .... **Diplura,** p. 228
 Tarsi 3-segmented; head having conspicuous eyes, as in fig. 216 **Dermaptera,** p. 252
28. Tarsus 4- or 5-segmented 29
 Tarsus 1- to 3-segmented 36
29. Base of abdomen constricted to a narrow joint hinged to forward part of body, figs. 279, 285 .... **Hymenoptera,** p. 312
 Abdomen not constricted and hinged at its base 30
30. Antenna minute, flattened, and indistinctly segmented, fig. 384, or round, sometimes with a terminal hair 31
 Antenna slender and long, many-segmented, figs. 210, 350 32
31. Antenna with many indistinct segments; both bilaterally compressed, with distinct segmentation; head and pronotum often with ctenidia, or rows of stout spines, fig. 384 .... **Siphonaptera,** p. 421
 Antenna globular, appearing as one segment, sometimes with a terminal hair; body not greatly compressed from side to side, and often without distinct segmentation on abdomen; never having ctenidia on head or pronotum, fig. 383 .... **Diptera,** p. 396
32. Head prolonged into a beaklike projection at the end of which are located a set of chewing mouthparts, as in fig. 267 .... **Mecoptera,** p. 311
 Head not prolonged into a beak 33

33. Mouthparts vestigial or composed chiefly of a short coiled tube, mandibles indistinct; body densely hairy or scaly, fig. 350 .... **Lepidoptera,** p. 372
Mouthparts having sclerotized and massive mandibles, mouthparts of simple chewing type, fig. 210; body never hairy 34
34. Pronotum enlarged, forming a long neck, fig. 203; a large saddle, fig. 210; or a shield partly or entirely hiding the head, fig. 201 .... **Orthoptera,** p. 239
Pronotum small, at most only slightly larger than mesonotum, fig. 219 35
35. Elongate sticklike insects, thorax as wide as or wider than abdomen, fig. 205 **Orthoptera,** p. 239
Stocky insects, thorax constricted and markedly narrower than either head or abdomen, fig. 219 .... **Isoptera,** p. 257
36. Head indistinct, antennae and legs short; insect body often covered by waxy filaments or plates, or by a detachable scale, fig. 260 ...... **Hemiptera,** p. 276
Head distinct; other characteristics diverse, but body never covered by a scale 37
37. Tarsus ending in a bladder-like pad; mouthparts together forming a conical structure, fig. 228 .... **Thysanoptera,** p. 270
Tarsus ending in claws which may be small and sharp or large and hooked, fig. 233 38
38. Mouthparts forming a distinct external tubular beak, figs. 235, 237 **Hemiptera,** p. 276
Mouthparts not forming an external beak 39
39. Pronotum forming a large sclerite, often saddle-shaped, and hind legs enlarged for leaping, fig. 210 .... **Orthoptera,** p. 239
Either pronotum reduced to a narrow sclerite, or hind legs not particularly enlarged 40
40. Antenna 13- to 50-segmented, fig. 225 .... **Corrodentia,** p. 265
Antenna 3- to 6-segmented 41
41. Leg having tibia and tarsus united, abdomen often having a ventral spring, fig. 190. Free-living species .... **Collembola,** p. 224
Leg having tibia and tarsus separate, articulating with a joint, fig. 233; abdomen never having a spring. Ectoparasites of warm-blooded animals and birds 42
42. Mouthparts of chewing type, with segmented palpi and sclerotized triangular teeth .... **Mallophaga,** p. 267
Mouthparts of sucking type, consisting of a bundle of stylets which are retractable into the head .... **Anoplura,** p. 273

Subclass Myrientomata

These are elongate six-legged wingless animals comprising the order Protura. They differ from all other insects in their type of growth, called *anamorphosis*. With anamorphosis segments are added to the body at successive molts. In the Protura a segment is added to the abdomen at each molt. The Protura have no antennae; this also distinguishes them from all other adult insects.

Order PROTURA

The adults are small and slender, fig. 189, ranging from 0.5 to 2 mm. in length. The head is cone-shaped; it has neither eyes nor antennae, but possesses well-developed chewing mouth-parts consisting of stylet-like mandibles, small and generalized maxillae, and a poorly developed membranous labium. The three pairs of thoracic legs are similar in general appearance; the first pair serve as tactile organs.

The nymphs are similar to the adults in general appearance. In growth they exhibit *anamorphosis,* that is, adding segments to the body at each molt. The abdomen of the first-stage nymph, the protonymph, has 9 segments; the abdomen of the deutonymph has 10 segments; that of the tritonymph has 11 segments; and, finally, the abdomen of the adult has 12 segments. The head and thorax are not affected in this manner.

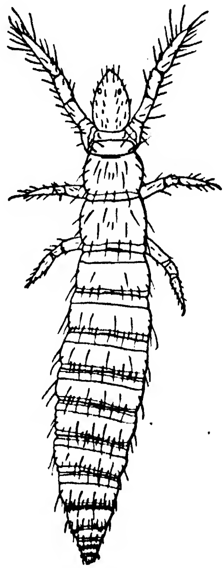

FIG. 189. *Acerentulus barberi.* (Redrawn from Ewing)

Proturans are moderately rare. They live in humus and soil, preferring damp situations. An ideal habitat for many species is old leaf mold along the edge of woods. Both adults and nymphs feed on decayed organic matter, and both may be found together during most of the year. Specimens may be collected either by examining leaf mold or by drying it in a Berlese funnel. Study specimens should be preserved in 70 per cent ethyl alcohol.

REFERENCE

EWING, H. E., 1940. The Protura of North America, Ann. Entomol. Soc. Am. **33**:495–551, illus.

Subclass Oligoentoma

This subclass includes only the order Collembola, a group of insects which have no obvious metamorphosis. The subclass is differentiated from other insects on the basis of three structural characters: (1) The abdomen is only six-segmented; (2) no definite genitalia are present in either sex; and (3) they lack Malpighian tubules. Of equal significance are the criteria of embryonic cleavage. In the Collembola, cleavage is holoblastic; that is, the entire egg is divided at the first cleavage. In other insects, cleavage is meroblastic; in the first cell divisions of the zygote the nuclei divide, but there is no corresponding division of the yolk mass of the egg into cellular compartments.

Order COLLEMBOLA

Springtails

Minute to medium-small wingless insects; with antennae and legs well developed; mouthparts of chewing type, but in some forms having

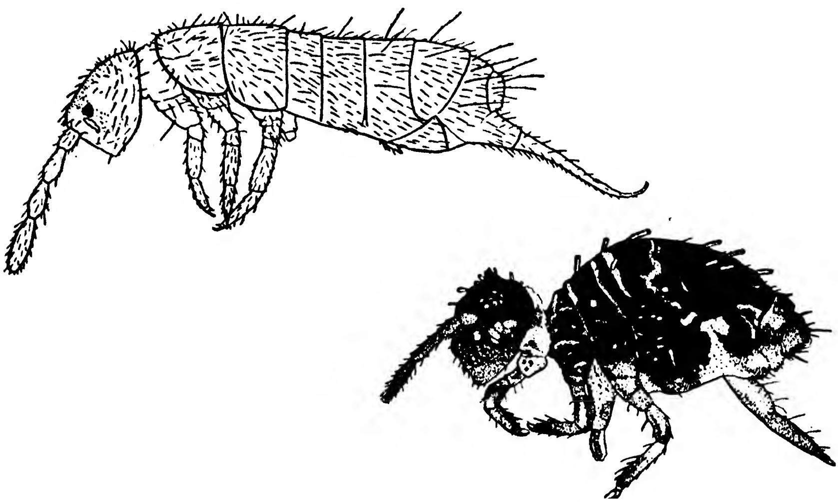

FIG. 190. Collembola. Above, *Isotoma andrei*, suborder Arthropleona; below, *Neosminthurus clavatus*, suborder Symphypleona. (After Mills)

the maxillae and mandibles long, sharp, and stylet-like; in the entire order the genae or cheeks have grown down and around the group of mouthparts, forming a hollow cone into which the mouthparts appear to be retracted. Abdomen frequently with a ventral jumping organ or furcula and a button-like structure, the tenaculum. Metamorphosis absent, both sexes usually similar and without definite genitalia.

The adults range in length from ⅕ mm. in the minute genus *Megalothorax* to over 10 mm. in the larger species of the Entomobryidae and Poduridae. In the suborder Arthropleona the body is long and cylindrical; in the suborder Symphypleona the abdomen is round and more or less globular, fig. 190. The antennae are four- to six-segmented, the last segment sometimes with many fine annulations. The eyes are either lacking or represented by a series of isolated ommatidia. Most members of the Collembola have a ventral springing organ or *furcula;* this is coupled with a ventral button or *tenaculum* when not in use. By means of the furcula these little animals can execute a leap of some distance, which has earned them their name of springtails. The young are similar to the adults in both appearance and habits, differing chiefly in size and sexual maturity. Many of the species are white or straw-colored, others are blue, gray, yellow, mottled, or marked with distinctive patterns.

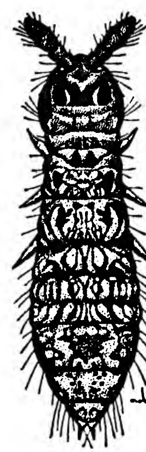

Fig. 191. *Achorutes armatus,* a springtail destructive to mushrooms. (From Illinois Natural History Survey)

Springtails are lovers of moisture and are found abundantly in many types of moist situations. Their favorite haunts include deep leaf mold, damp soil, rotten wood, the edges of ponds or streams, and fleshy fungi. A few species attack plants, especially members of the family Sminthuridae, and may be of local economic importance. A small gray species, *Achorutes armatus,* fig. 191, is sometimes destructive to mushrooms in commercial production. Egg-laying habits are known for only a few species, which lay their eggs singly or in clusters in humus or soil.

One of the most interesting features of the Collembola is their wide distribution. In a recent monograph by H. B. Mills, 132 species are listed from Iowa. Of these, 59 species, or 45 per cent, are holarctic or cosmopolitan.

Reference

Mills, H. B. A monograph of the Collembola of Iowa. Ames, Iowa, Collegiate Press, Inc. 143 pp., 189 figs.

Subclass Euentoma

This subclass includes the great majority of insects, different groups exhibiting a wide range of structural and biological characteristics. The abdomen is usually nine- or ten-segmented; definite genitalia are usually developed; and Malpighian tubules are present, often in great numbers. Embryological development is meroblastic; that is, only the nuclear material is divided in the first cleavages of the zygote. The

Euentoma have various types of metamorphosis, but not anamorphosis, as exhibited by the subclass Myrientomata.

The Euentoma are divided into two major groups: the *Apterygota* and *Pterygota*. The Apterygota include two small orders: Thysanura (bristletails) and Diplura (campodeids and japygids), which appear to represent primitive insects before wings had made their appearance in the insect group. This antiquity of origin is indicated by extremely primitive characteristics of both a morphological and biological nature. The Pterygota are the winged insects. Included in the Pterygota are a number of orders which have no wings, such as the fleas and lice. Morphological or biological evidence either indicates very strongly or proves that these wingless groups are close relatives of winged orders and that their ancestors possessed wings. Their present wingless condition is therefore considered to be due to degeneration.

The Pterygota are divided into two large groups on the basis of metamorphosis. Many orders, such as Orthoptera and Hemiptera, develop from egg to adult by gradual or incomplete metamorphosis and are grouped together under the name *Hemimetabola*. The orders having complete metamorphosis are termed the *Holometabola* and include the Coleoptera (beetles), Hymenoptera (bees), the Lepidoptera (moths and butterflies), Diptera (true flies), and several smaller orders (see Table 2, p. 53).

APTERYGOTA

This group, represented by the Thysanura and Diplura, is characterized by the completely wingless condition. Metamorphosis is not conspicuous, the young resembling the adults very closely except in size. Primitive features include not only the type of metamorphosis and wingless condition but also the following: (1) segmentally arranged gonads (see p. 116); (2) undivided platelike tergites on each of the three thoracic segments; (3) poorly developed pleural sclerites; and (4) the presence of rudimentary appendages on the abdomen in the Thysanura. Both orders have well-developed legs, antennae, cerci, and chewing-type mouthparts.

Order THYSANURA

Silverfish, Bristletails, Firebrats

Wingless soft-bodied insects, small to medium size, with long multisegmented antennae, distinct cerci, and a long caudal filament, fig.

192. Mouthparts of chewing type. Abdomen with vestigial appendages. Metamorphosis inconspicuous.

The young and adults are extremely similar in shape and habits, differing chiefly in size and sexual maturity. Eyes vary greatly, large in some forms, minute or absent in others. The legs are stout, hairy, short, and flattened laterally. The body is slender and tapers posteriorly. All species are extremely swift runners and agile dodgers. The abdomen has vestigial paired appendages, represented by plate-like coxopodites (which look like part of the sternite) and a finger-

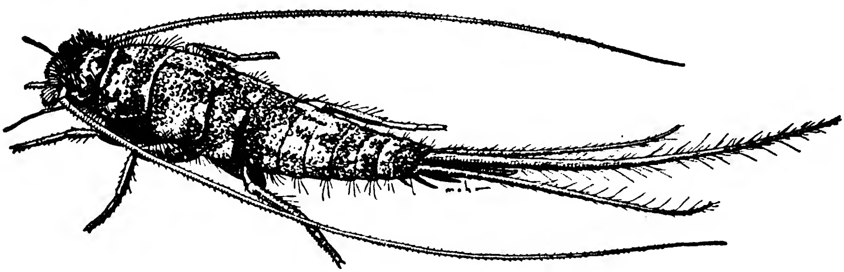

FIG. 192. Thysanura. *Thermobia domestica,* a common silverfish. (From Illinois Natural History Survey)

like stylet projecting from the posterior margin of the coxopodite. There are 10 complete abdominal segments; the 11th forms the caudal filament.

Outdoor species feed on humus and other organic matter and are found among leaves and around stones; the genus *Machilis* (which has large eyes) also frequents moist shaded rock outcrops. The family Ateluridae contains a few small ovate forms which live in ant nests. The most widely known species are the domestic silverfish and firebrats. Little is known about many details of their life history. It is thought that they lay eggs singly in cracks and crevices. The young go through several molts before becoming adult. The outdoor species hibernate as adults in ground cover.

Economic Status. Silverfish, *Lepisma saccharina,* firebrats, *Thermobia domestica,* and other domestic species feed commonly on starch. They cause considerable damage to books and clothing by chewing off the starch sizing; other articles containing glue or sizing are attacked.

REFERENCES

See under Diplura.

Order DIPLURA

Campodeids and Japygids

Wingless blind slender insects of small size, with long, many-segmented antennae, well-developed legs, with a pair of conspicuous cerci which are either segmented or forceps-like. Mouthparts of

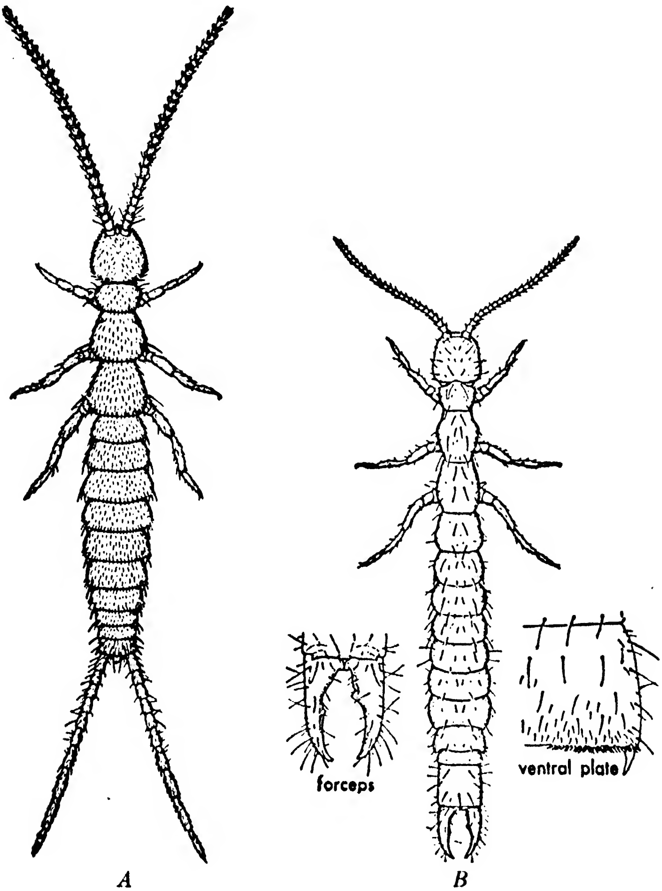

Fig. 193. Diplura. *A, Campodea folsomi; B, Japyx diversiungius.* (From Essig, "College Entomology," by permission of The Macmillan Co.)

chewing type hidden within the ventral pouch of the head. Metamorphosis not marked.

The young and adults differ chiefly in size and sexual maturity. The genae of the head have outgrowths that form the ventral pouch in which the mouthparts are situated. The legs are not so well developed as in the Thysanura, and the abdomen has neither vestigial paired appendages nor a caudal filament. In the Campodeidae, fig. 193*A*, the abdomen has a pair of many-segmented cerci; in the Japygidae, fig. 193*B*, the cerci are forceps-like.

The species of the order occur under leaves, stones, logs, or debris, or in the soil. Their movements are at most moderately rapid, and they seldom if ever come out into the light. Practically nothing is known about details of their life history; none of the species is of economic importance.

Reference

Escherich, K., 1904. Das System der Lepismatiden, Dem Gesamtgebiete der Zoologie **43**:1–164, illus.

PTERYGOTA

To this group belongs the great variety of winged insects and certain orders such as the fleas which have lost their wings by degeneration. Unlike the Apterygota, which includes only two fairly similar orders, the Pterygota embraces a varied assemblage representing many diverse types of insects. The mouthparts represent chewing, sucking, sponging, and other types; and both gradual and complete metamorphosis occur in the group.

The various orders of the Pterygota are divided into two principal series on the basis of their type of metamorphosis. In one group, exemplified by grasshoppers and true bugs, metamorphosis is gradual or incomplete. This series is the *Hemimetabola*. In the other group, the *Holometabola*, metamorphosis is complete, with larval and pupal stages developed. Moths and wasps are examples of the *Holometabola*.

Series Hemimetabola

This series contains fourteen living orders. In two of these orders, the Ephemeroptera (mayflies) and Odonata (dragonflies and damselflies) the wings cannot be folded and laid rooflike over the back and hence in repose are held either straight out from the sides or vertically above the thorax. It is believed that this group represents the most primitive and ancient known type of flying insect, and is called the Palaeoptera. Several orders of Palaeoptera occurred in the late Paleozoic era, but only the two mentioned have persisted to the present time. The immature stages of the extinct orders were apparently aquatic, as are those of their present-day relatives. Of special interest is the extinct order Protodonata, which is a close relative of the Odonata and contained the largest known insect, *Meganeuron*, fig. 391, with a wing spread of 29 inches.

In the other winged orders of Hemimetabola, the wings can be folded and in repose laid over the back. This group is called the Neoptera and is considered as representing a distinct advance in the development of wing mechanics among insects.

Of the hemimetabolous orders of Neoptera, the Orthoptera are the most primitive, judged by the generalized structure of the mouthparts and the net-veined wings. The orders Isoptera, Plecoptera, and Dermaptera are close relatives of the Orthoptera. The Zoraptera, Embioptera, Corrodentia, and the wingless order Mallophaga also appear to belong in the orthopteroid complex because they have mandibulate chewing mouthparts. The remaining three orders, the Anoplura, Hemiptera, and Thysanoptera, form a group in which the mouthparts are of the piercing–sucking type. Except for the functional similarity of their mouthparts, these three orders are extremely different and have few characters in common.

Order EPHEMEROPTERA

Mayflies

Small to large, soft-bodied, slender insects with gradual metamorphosis. Adults having two pairs of net-veined wings, the metathoracic pair small, completely atrophied in a few genera; legs usually well developed; antennae inconspicuous and hairlike; mouthparts vestigial; eyes large; and abdomen with a pair of cerci and in many species with a median terminal filament all very long and taillike, fig. 194. Nymphs aquatic, varied in shape, and similar in general structures to adults, but with well-developed chewing mouthparts; and usually with series of tracheal gills on the abdomen, fig. 194.

Metamorphosis in the mayflies is characterized by a feature unique among insects. The nymphs follow the usual type of gradual development with wings developing in external pads. When full grown, they swim to the surface of the water or crawl up on some support, and the winged form escapes from the nymphal skin. This winged form is capable of flight and looks like an adult but in reality is not yet sexually mature. The term subimago is applied to this stage. A day

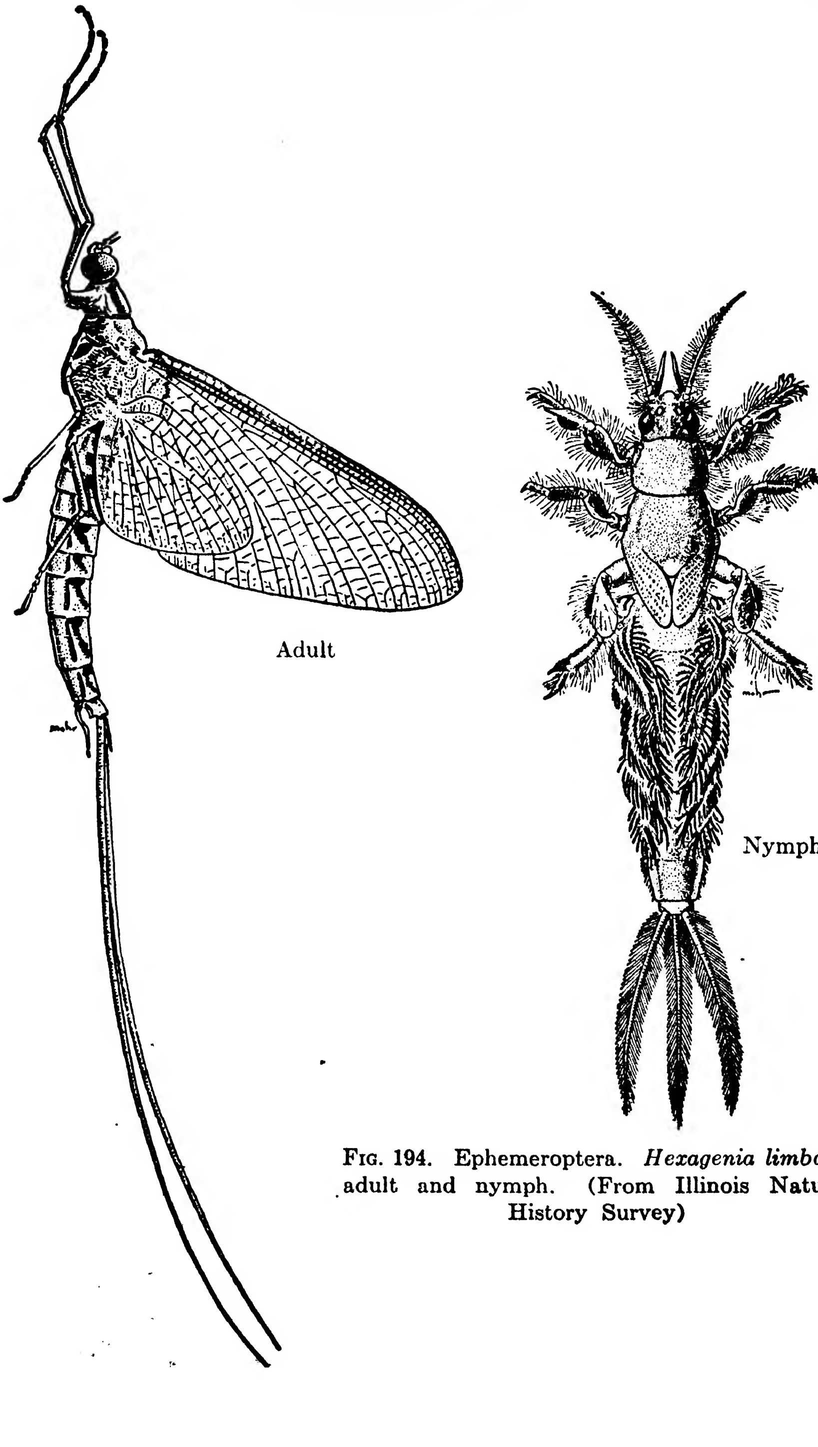

Fig. 194. Ephemeroptera. *Hexagenia limbata,* adult and nymph. (From Illinois Natural History Survey)

or two after emergence, it molts again and produces the mature adult. The adults apparently take no solid food, probably imbibing only water during their short life. In certain genera, especially *Hexagenia* and *Ephemera*, mass emergence of adults may take place, resulting in the appearance of clouds of these insects over lakes and along

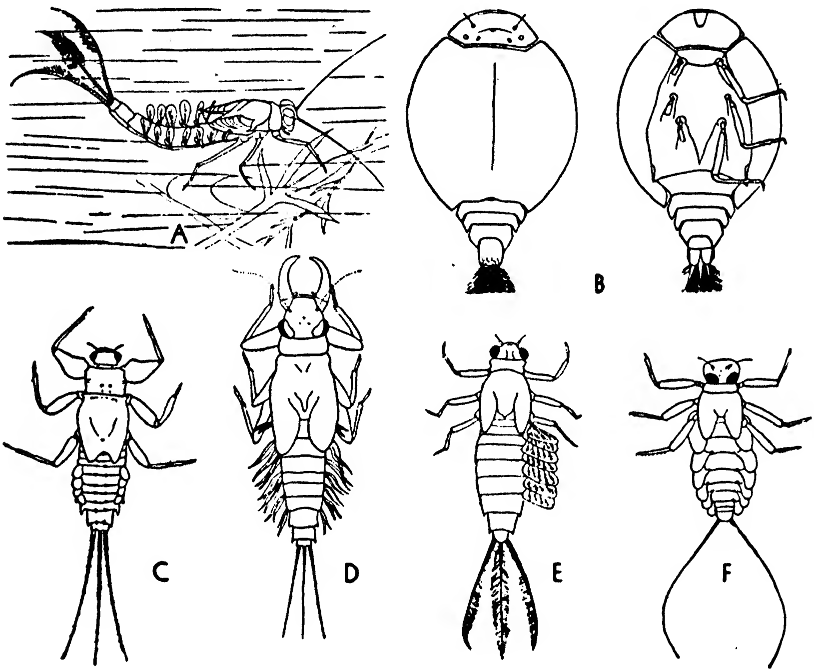

FIG. 195. Nymphs of mayflies. *A, Callibaetis fluctuans; B, Prosopistoma foliaceum,* dorsal and ventral aspects; *C, Ephemerella grandis; D, Paraleptophlebia packii; E, Siphlonurus occidentalis; F, Iron longimanus.* (From Essig, after various sources, "College Entomology," by permission of The Macmillan Co.)

streams. The adults mate in dancing swarms. The female extrudes masses of eggs from the abdomen, swoops down to the water and releases the eggs into it. Each female may lay several hundred to several thousand eggs.

The complete adult life of many species of mayflies is extremely short, lasting at most only a few days; mating normally occurs the same day adulthood is achieved, and the eggs are laid almost immediately. These eggs hatch in a few weeks or a month. In certain genera, such as *Callibaetis* and *Cloeon,* the adult females live much longer, from 2 to 3 weeks. In these longer-lived forms the eggs are fertilized and held in the body until the embryos are mature. When laid, the eggs hatch almost immediately on touching the water.

Nymphs, fig. 195, live in a great variety of lake, pond, and stream situations. The nymphs of some species mature in 6 weeks; others may require 1, 2, or 3 years to attain their full growth. Their food consists of microorganisms and fragments of plant tissue.

The nymphs of the family Hexageniidae live in mud, burrowing through it by means of their large shovel-like front legs. Many nymphs of other families occur under stones and logs. Those which live in rapid mountain streams may have the entire venter of the body developed into a disclike suction cup which enables them to attach firmly to smooth surfaces. Nymphs of a few genera live in small pools or ponds and are free swimmers along the bottom or in the shallows.

Mayflies play an extremely important role in the fish-food economy of most North American waters. They are the most abundant insect group in many types of fishing waters. Studies of fish-stomach contents indicates that, by and large, mayflies and chironomids (midges) are undoubtedly the two most important insect groups from the standpoint of fish food.

Reference

Needham, J. G., J. R. Traver, and Yin-chi Hsu, 1935. The biology of mayflies. Ithaca, N. Y., Comstock Publishing Co., Inc. 759 pp., 169 figs.

Order ODONATA

Dragonflies and Damselflies

Medium-sized to large predaceous insects with gradual metamorphosis. Adults slender or stout-bodied, with two pairs of nearly similar net-veined wings; legs well developed; antennae hairlike; mouthparts mandibulate, of the chewing type; eyes large; abdomen without long "tails." Nymphs aquatic; mouthparts of chewing type, with labium elongate and hinged to form a stout grasping organ for seizing prey; legs stout; three leaflike terminal gills present in the suborder Zygoptera.

All the adult Odonata feed on insect prey captured on the wing. They devour mosquitoes, midges, horseflies, in fact, almost any insect that the odonate can tackle and catch successfully. The nymphs are

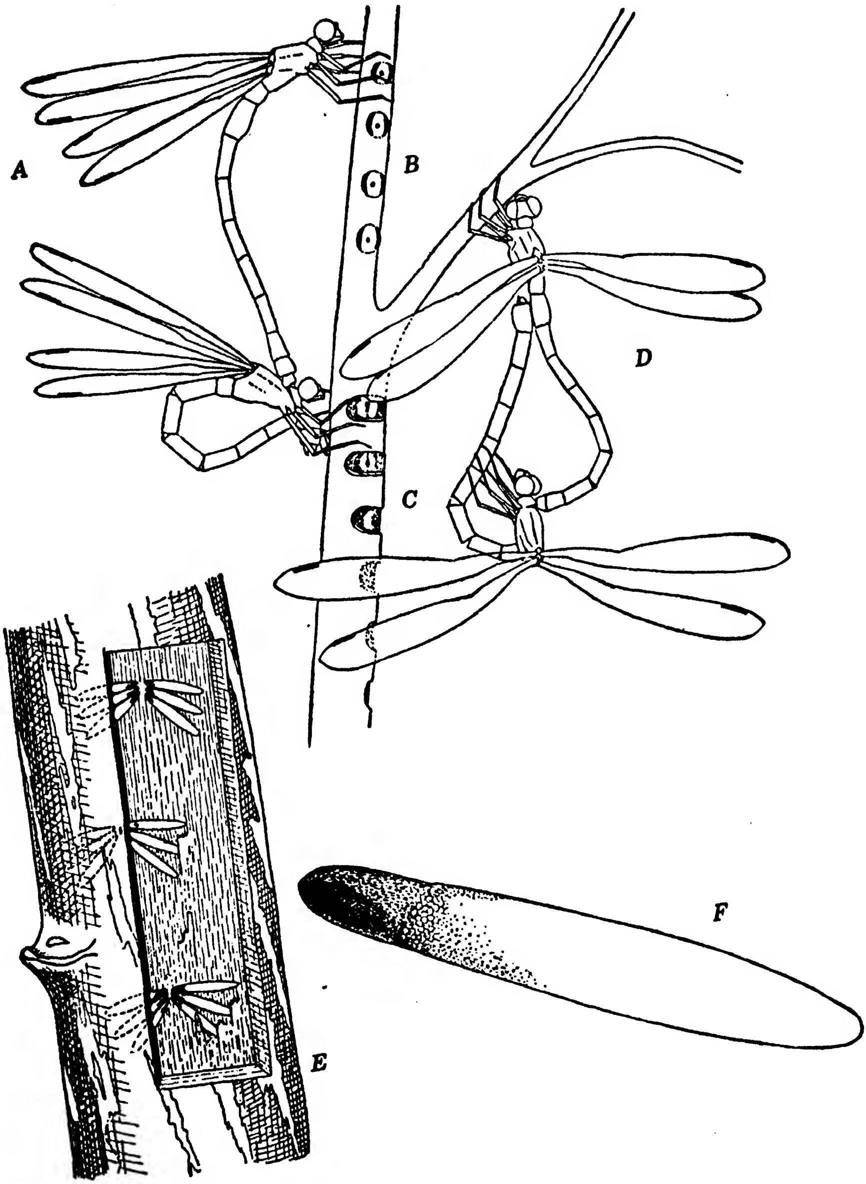

FIG. 196. Habits of the damselfly *Archilestes californica*. *A*, ovipositing; *B*, scars from oviposition, one year old; *C*, scars two years old; *D*, in copulation; *E*, bark cut away showing eggs in cambium; *F*, egg. (After Kennedy)

aquatic, living chiefly in ponds, lakes, and backwaters of streams. They do not swim, but instead walk along the bottom or among debris or vegetation. The nymphs like the adults are predaceous, catching aquatic insects, crustaceans, and the like, trapping them with the extensile spined labium.

The eggs are laid in or near the water in a variety of ways. Some are thrust into aquatic vegetation or rotten wood; others may be deposited in masses on some object just beneath the water surface, or laid in ribbons or rings in the water, or thrust into wet mud near the water's edge. Females of many species dip down to the surface and wash the eggs off the end of the abdomen. Others crawl beneath the water to deposit eggs.

Nymphs of the smaller species mature in a year. In the case of larger species, development may take 2 to 4 years. Hibernation is passed in the nymphal stage. When full grown, the nymphs crawl out of the water and attach to a stick, stem, or other object for the last molt. The newly emerged adults harden and color relatively slowly, many of them requiring 1 or 2 days for the process.

A peculiar characteristic of the order is the method of mating, fig. 196. Before mating, the male bends the tip of the abdomen forward and transfers the spermatozoa to a bladder-like receptacle situated in the second abdominal sternite. In mating, the male, using its terminal claspers, grasps the female around the neck; the female then bends her abdomen forward to the second sternite of the male, at which place the actual transfer of spermatozoa is effected. This unusual procedure is known in no other order of insects.

The Odonata includes three different types of insects which look and act strikingly different but which are separated by only a limited number of diagnostic characters. Present-day forms of one suborder, Anisozygotera, are known to occur only as rarities in the oriental region. The two suborders which occur in North America may be separated by the following key.

Diagnosis of Suborders

Nymphs provided with terminal leaflike tracheal gills, fig. 198. Adults having fore and hind wings of similar shape and venation, when at rest held together and extending parallel to the abdomen, fig. 197...... Zygoptera, damsel flies

Nymphs without external gills, fig. 200. Adults with hind wings much wider than fore wings, especially at the base, extended outwards when at rest, fig. 199 Anisoptera, dragon flies

Suborder ZYGOPTERA

Damselflies

Damselflies are always slender and delicate, with a fluttering flight quite in contrast to the rapid and positive movements of the dragonflies. The damselfly adults have a thorax of very peculiar shape, fig.

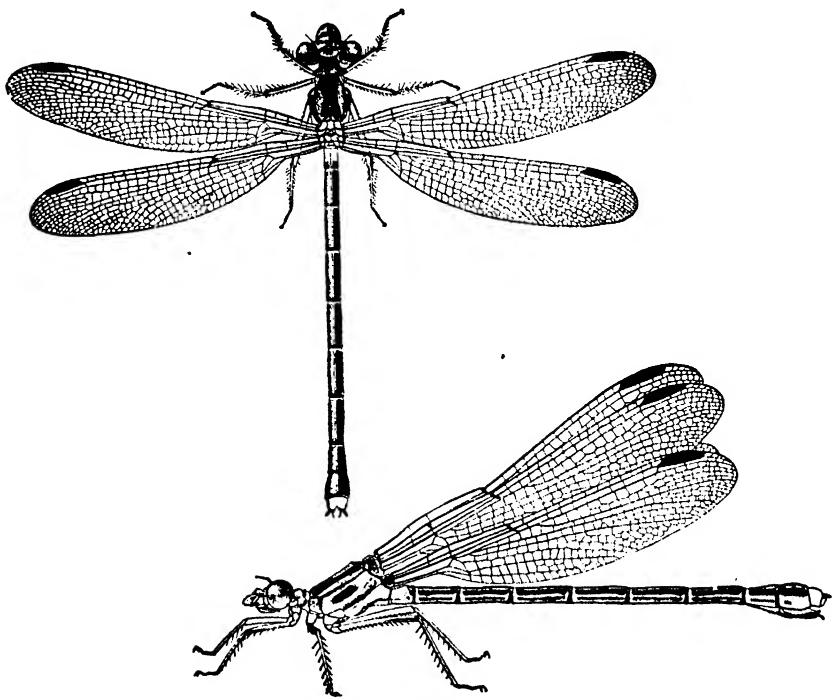

Fig. 197. A damselfly *Archilestes californica.* (After Kennedy)

197; the meso- and metathorax together are somewhat rectangular and tilted backwards 70 or 80 degrees in relation to the linear axis of the entire body. The wings at rest are held together above the back at right angles to the upper margin of the meso- and metathorax. Because these are tilted to such a degree, the folded wings are nearly parallel to and held just above the abdomen.

Most of our adults are somber-hued, but a few have red or black banding on the wings or metallic green or bronze body and wings.

The nymphs, fig. 198, are also slender and possess three large caudal tracheal gills. They frequent the stems of aquatic vegetation more than the actual bottom of ponds or streams.

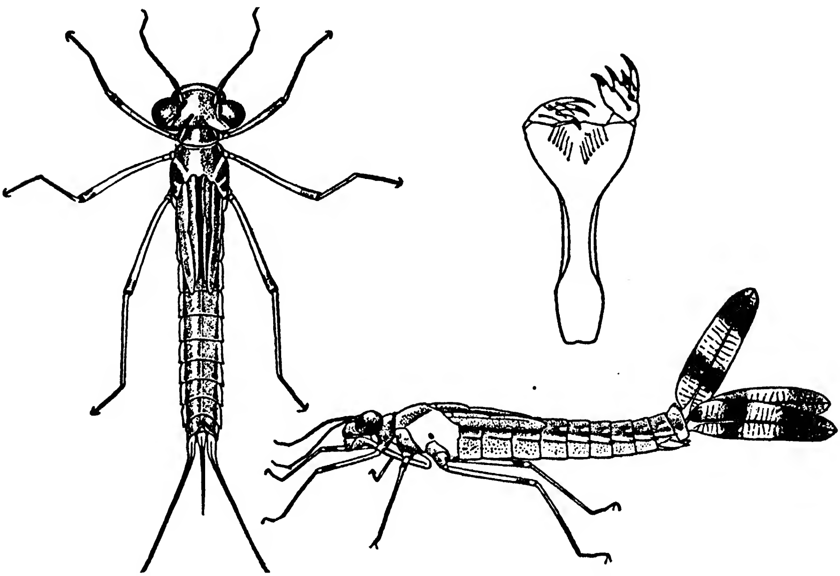

FIG. 198. A damselfly nymph *Archilestes californica.* Insert is labium showing grasping teeth. (After Kennedy)

Suborder ANISOPTERA

Dragonflies

The adults of this suborder, fig. 199, are stout bodied, with strong, graceful, and superbly controlled flight. The thorax is not tilted as in the damselflies, and the wings at rest are extended to the side. Many species are gaudily colored and have conspicuous mottling or spotting on the wings. Older specimens frequently develop a pale-blue waxy bloom over the body and wings which may obscure the original colors and markings.

The adult members, especially the larger ones, are great favorites with the out-of-doors enthusiast. Few of the dragonflies are gaudily colored, but their flight is of such speed and poise as to entrance the spectator. Each dragonfly has a regular beat. Up and down this it flies, patrolling the beat at regular intervals, and looking for flying insects as prey. When one of these is sighted, the dragonfly wheels from its course in pursuit of the prey; when the prey is captured, the dragonfly wheels back to its regular beat. Sometimes rivals clash, and there is displayed a real show of aerial acrobatics to the accompaniment of clicking of mandibles and rustle of wings.

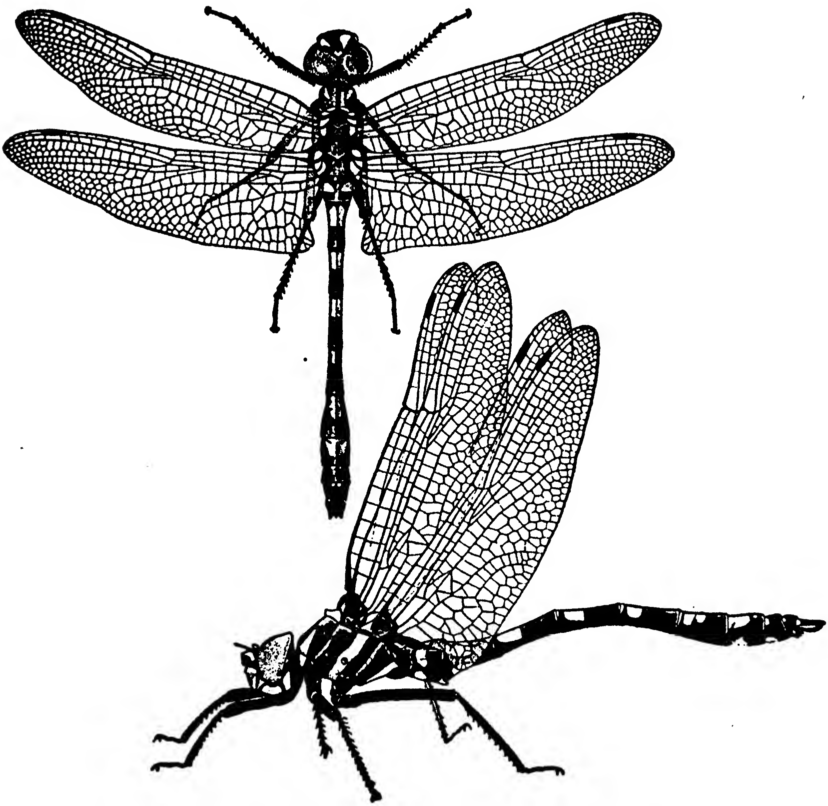

Fig. 199. A dragonfly *Macromia magnifica*. (After Kennedy)

The nymphs, fig. 200, are also stout, many of them frequenting the ooze or mud in the bottoms of ponds and lakes. They have no external gills but have a rectal respiratory chamber (see p. 151) in which the gaseous exchange takes place. Such a respiratory chamber is found in no other group of insects.

References

Garman, Philip, 1927. The Odonata or dragonflies of Connecticut, Conn. Geol. Nat. Hist. Surv. Bull. **39**, 331 pp., 67 figs., 22 pls.

Needham, J. G., and H. B. Heywood, 1929. A handbook of the dragonflies of North America. Springfield, Ill., C. C. Thomas. 378 pp., illus.

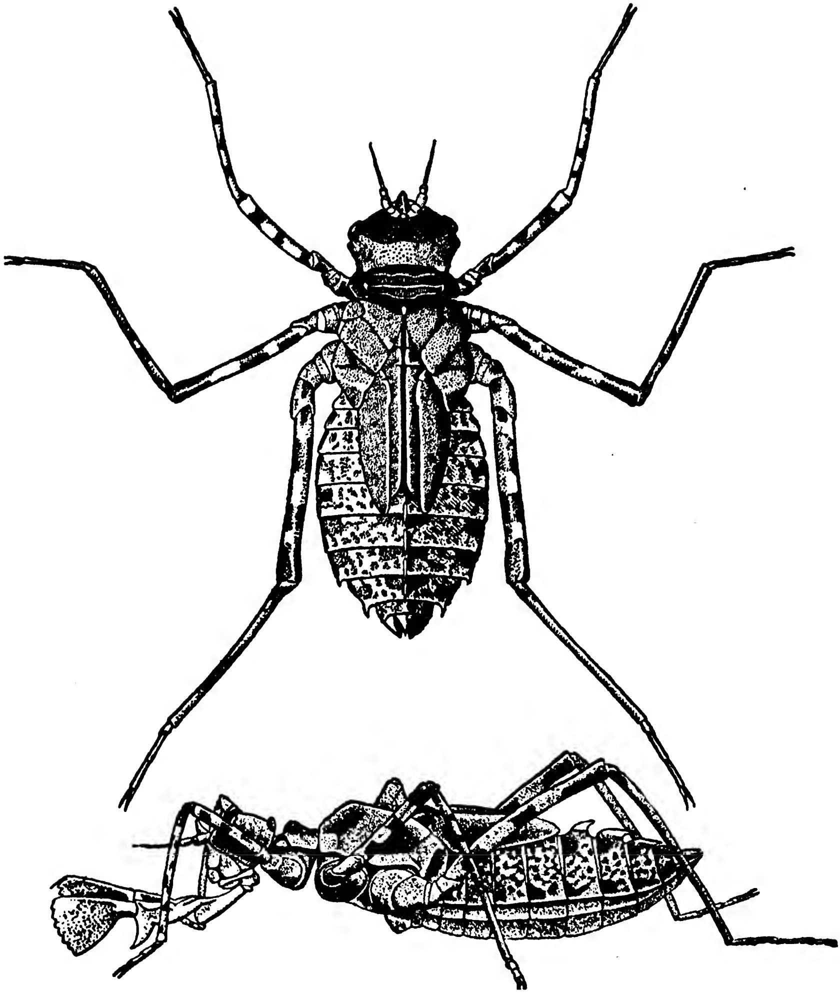

FIG. 200. A dragonfly nymph *Macromia magnifica*. (After Kennedy)

Order ORTHOPTERA

Cockroaches, Grasshoppers, and Allies

In this order belongs a varied assemblage of insects, including wingless, short-winged, and long-winged forms. The winged forms have two pairs of net-veined wings: the fore wings, called *tegmina*, are leathery or parchment-like; the hind pair are membranous, larger, and folded beneath the tegmina in repose. The head bears antennae, eyes (rarely vestigial), and mouthparts of a generalized chewing type. Metamorphosis is gradual. Adults and nymphs are terrestrial.

The order Orthoptera contains the cockroaches, fig. 201, the walkingstick insects, fig. 205, praying mantids, fig. 203, and the grasshoppers and crickets. A glance at the illustrations will show that they differ greatly in appearance, owing to varying proportions of parts of the body and appendages. The fundamental structure, however, is very similar throughout the order, as exemplified by the uniform type of chewing mouthparts, similar type of wing venation, and many similarities of internal organs. The order may be separated into five suborders that may be identified by means of the following key.

Key to Suborders

1. Front legs large, with series of strong teeth on opposing tibia and femur, fitted for grasping prey, fig. 203; pronotum elongate ...... **Mantodea,** p. 243
   Front legs either similar to middle legs in general shape, or with large claw-like digging "fingers" on tibia and tarsus, fig. 213 2
2. Pronotum wider than long, only slightly convex, its front margin and sides forming extensive flanges which extend over the head and the base of the legs, fig. 201; broad flat insects having legs well developed for running **Blattaria,** p. 240
   Pronotum either longer than wide or without expanded areas; frequently the pronotum forms a saddle-like structure, fig. 206; the hind legs are often enlarged for jumping 3
3. Abdomen having long 8- or 9-segmented cerci; slender insects without wings, fig. 215 .... **Grylloblattodea,** p. 252
   Abdomen having cerci 1- or 2-segmented, usually short and inconspicuous, fig. 211 4
4. Elongate, apterous insects having long slender legs, mimicking sticks, fig. 205 **Phasmida,** p. 244
   Much more robust insects as in figs. 206, 212, in which either the hind femora are enlarged for leaping or wings are present .... **Saltatoria,** p. 245

Suborder BLATTARIA

Cockroaches

Cockroaches are rapid-running flattened insects, with long slender antennae, well-developed eyes, and chewing mouthparts having mandibles, maxillae and labium very similar in type to figs. 68, 69, and 70, respectively. In species with well-developed wings, fig. 201, both pairs have many veins and a very large number of crossveins; the fore pair are narrower, thickened, and leathery or parchment-like, called *tegmina,* serving chiefly as a cover for the hind pair when not flying; the hind pair are thin, much larger, used chiefly in flight, and are folded fanlike beneath the tegmina when not in use. Many species have only padlike wings or no wings at all. The prothorax is large and conceals much of the head. The abdomen is large, many segmented, and bears a pair of apical cerci.

This suborder contains only one family, the Blattidae. In North America it is represented by about seventy species. More than two thousand species are known for the world.

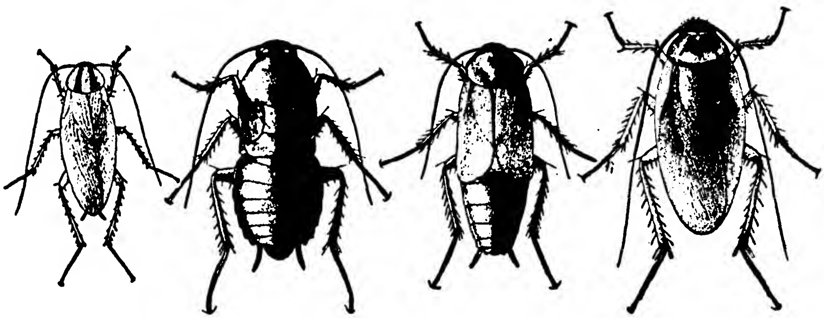

FIG. 201. Common cosmopolitan cockroaches. The German cockroach *Blatella germanica;* the Oriental cockroach *Blatta orientalis,* female and male; and the American cockroach *Periplaneta americana.* (From Connecticut Agricultural Experiment Station)

Cockroaches frequent dark humid situations. Typically they belong to the tropics, where occurs a great variety of species, large and small. An extensive native fauna occurs in the southern portion of the United States, especially in humid regions. A limited number of outdoor species are found in the areas to the north, where they occur chiefly under bark of dead trees or fallen logs. The more conspicuous elements of the cockroach fauna of the northern states are not native to this continent but are a group of cosmopolitan species that are household pests. They find in human dwellings and heated buildings the semitropical conditions which enable them to thrive and multiply throughout the entire year. They are almost omnivorous in habit, eating a wide variety of animal and vegetable foods. The nymphs are similar to the adults in general structure and usually occur and feed along with the adults. In certain species in which wings are never developed, it is sometimes necessary to examine the genitalia to differentiate adults and nymphs.

The egg-laying habits of cockroaches are unusual. As the successive individual eggs are extruded from the oviduct they are grouped in an egg chamber and "glued" together by a secretion into a capsule or *oötheca.* These are definite in shape and sculpture for the species. The eggs in each usually number 15 to 40, arranged in symmetrical double rows, fig. 202. The oötheca is formed over a period of several days and the end gradually extruded beyond the abdomen. The female carries the oötheca attached to the abdomen until the eggs are almost ready to hatch. The actual hatching occurs in some warm dark moist spot where the female has deposited the oötheca.

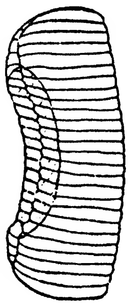

FIG. 202. Oötheca of *Blatella germanica,* with lateral portion cut away to show arrangement of individual eggs.

The nymphs are extremely active but grow relatively slowly. The smaller species may attain maturity in a few months, but the larger species may require a year or more. Many species are gregarious in habit, the adults and nymphs running together.

Of unusual interest is the wood roach *Cryptocercus punctulatus* found in the southeastern states. The species lives in colonies in decaying logs and has developed a close approach to true social life. The family unit forms the colony, several generations living together. The species feed on rotten wood. The first steps in the digestion of this cellulose material are accomplished by certain Protozoa, which are always abundant in the intestinal fauna of *Cryptocercus.*

Economic Importance. Cockroaches are one of the most disagreeable pests of human habitations. They get into many kinds of food, eat part of it, discolor and spot it with fecal material, and leave behind a disagreeable odor. In addition to the actual spoilage they cause, these scurrying insects are regarded as a general nuisance and a sign of unclean conditions. As a consequence the nation foots a large bill for the control of these insects in warehouses, eating places, and homes.

North of the frost line three cosmopolitan domestic species are most abundant, the small German cockroach *Blatella germanica,* the larger Oriental cockroach or "water bug" *Blatta orientalis,* and the American roach *Periplaneta americana,* the largest of the three and sometimes nearly as big as a small bat. In local areas the Australian cockroach *Periplaneta australasiae* is abundant; this is another cosmopolitan species as large as the American roach. To the south of the frost line other more tropical species invade buildings, some species attaining the size of a mouse.

Suborder MANTODEA

Praying Mantids

Predaceous insects of medium to large size, having an elongate prothorax and large spined grasping front legs, fig. 203. The middle and hind legs are usually slender. Otherwise the mantids are similar in general features to the cockroaches. Indeed, the structure of their mouthparts, internal organs, and genitalia indicates that the mantids

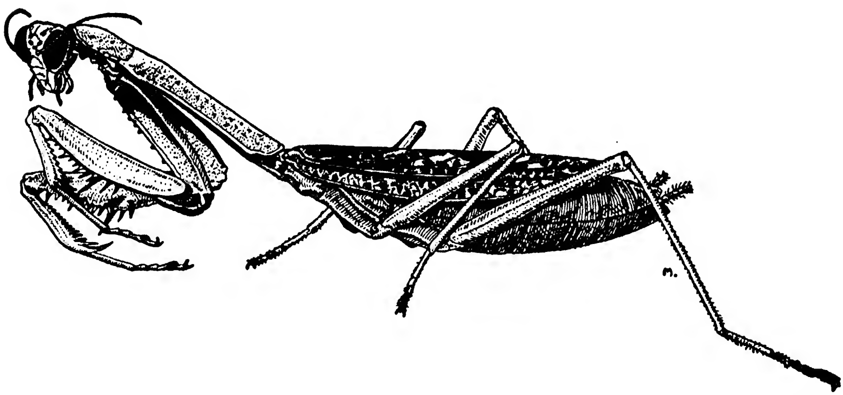

FIG. 203. A praying mantis *Stagmomantis carolina*. (From Illinois Natural History Survey)

are closely related to the cockroaches, in spite of the striking differences between the two in general appearance. The mantids comprise a single family, the Mantidae, represented in North America by only a few dozen species. As with the cockroaches the tropics support a larger fauna. Two species in the North American mantid fauna were introduced, *Mantis religiosa* from Europe and *Paratenodera sinensis* from the Orient. Both species probably came into the United States as oöthecae on nursery stock or packing.

The mantids may be long-winged, short-winged, or completely wingless. Many are green, brown, or mottled; a few species have brighter colors, and some have definite patterns.

All the species are predaceous in habit, feeding on other insects which they capture by means of the prehensile front legs. Cannibalism is not unusual, in fact, in certain species it is customary for the female to seize and devour the male after mating is completed.

Mantid eggs are deposited in large masses of definite pattern. In these masses or oötheca the eggs are arranged in a series of rows, glued together with secretion, and the whole mass glued to a branch or other object, fig. 204. In the northern areas there is single generation per year, and the winter is passed in the egg stage. It is interesting to gather these oötheca in late winter or early spring and bring them into the laboratory, and see the young mantids emerge sometime later. The eggs are frequently parasitized by some Hymenoptera

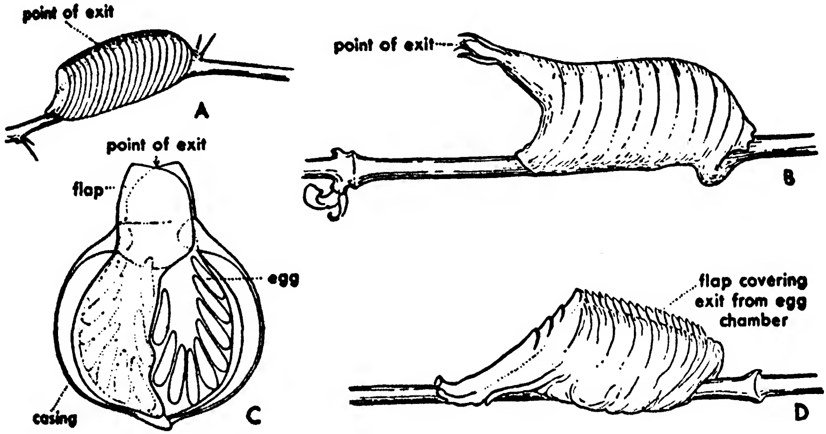

FIG. 204. Mantid oöthecae or egg capsules. *A*, generalized type; *B*, *Oligonyx mexicanus*; *C*, sectional and *D*, exterior aspects of *Paratenodera sinensis*. (From Essig, "College Entomology," by permission of The Macmillan Co.)

which are as odd looking as the young mantids; the parasites normally emerge from the oötheca some time after the hatching date of the mantids.

Suborder PHASMIDA

Walkingstick Insects

Large sluggish insects which are either leaf mimics or stick mimics, fig. 205. The North American species are wingless, except for a single Florida species, *Aplopus mayeri*. The resemblance of so many species to sticks has given the suborder the name "walkingstick insects." The head is round and has long slender antennae, small eyes, and simple chewing mouthparts. The body and legs are long, sometimes thorny or extremely slender. The smaller species may be only ½ inch long (over 12 mm.); the largest, the southeastern *Megaphasma dentricus*, attains a length of 6 inches (125 to 150 mm.). Some of the tropical species are broad and leaflike, with leaflike expansions on the leg segments.

All members of the phasmids are leaf feeders, most of them frequenting trees. They sometimes are sufficiently abundant to defoliate large areas of woodland. The insects themselves are never conspicuous. Their sticklike appearance and green or brown coloring gives them almost perfect protection from observation without close scrutiny. They move very slowly and feign death if disturbed.

The eggs are laid singly and simply dropped, falling to the ground. The winter is passed in this stage, the adults dying with the advent of cold weather. There is only one generation a year.

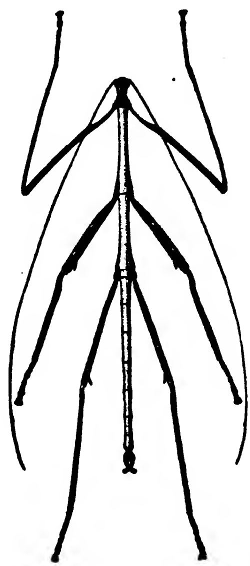

Fig. 205. A walking-stick *Diapheromera femorata*. (From Illinois Natural History Survey)

Suborder SALTATORIA

Grasshoppers and Crickets

Medium-sized to large insects having the hind legs elongate, their femora enlarged for leaping, fig. 206. In almost all forms the pronotum is large and produced downward at the sides to form a large collar back of the head. The head is large, with long antennae, well-developed eyes, and chewing mouthparts of a simple type. In many species the wings are large and functional; the tegmina are invariably leathery, and the hind wings membranous, pleated fanwise in repose. Other species may be short-winged or completely wingless.

To the Saltatoria belong the grasshoppers, crickets, katydids, mole crickets, and pygmy locusts, altogether making up an array of forms varied in size, shape, color, and habits. Seven or eight families usually are recognized in the North American fauna, including several hundred species.

Key to Common Families

1. Front tibiae and tarsi enlarged for digging, the former having a group of large heavy sharp processes, the latter forming two or more heavy flanged knifelike processes, fig. 213 .... **Gryllotalpidae,** p. 250

   Front tibiae and tarsi lacking heavy black processes 2
2. Hind tarsi minute or absent, but the tibial spurs forming large flat structures (used for jumping on mud), fig. 214 .... **Tridactylidae,** p. 250

   Hind tarsi well developed, projecting beyond tibial spurs, figs. 206, 211 3

3. Antennae much shorter than body and relatively heavy, fig. 206 4
   Antennae much longer than body, slender, fig. 209 5
4. Pronotum extending backward into a long shield covering all or nearly all of abdomen; tegmina short and ovate, fig. 207 .... **Tettigidae,** p. 247
   Pronotum extending only over thorax, tegmina various but often extending beyond apex of abdomen, fig. 206 .... **Locustidae,** p. 246
5. Tarsi 4-segmented .... **Tettigoniidae,** p. 247
   Tarsi 3-segmented .... **Gryllidae,** p. 250

Locustidae. This family contains the grasshoppers and migratory locusts, fig. 206. The antennae are short, seldom half the length of the body, and, because of this characteristic, the family is often called

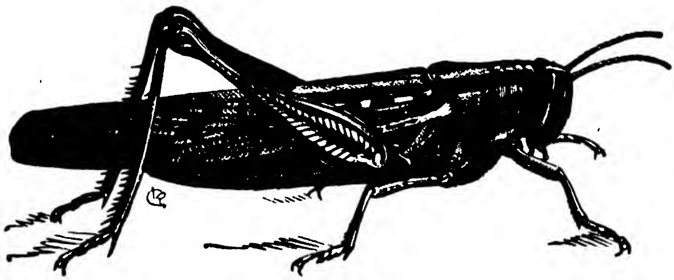

FIG. 206. The bird grasshopper *Schistocerca americana americana.* (From Illinois Natural History Survey)

the short-horned grasshoppers. Most of the group are grass or herb feeders, but a few feed on the foliage of trees. The eggs are deposited in masses in the soil. The female works the end of the abdomen down into the soil to form a chamber; into the end of this chamber she starts depositing eggs, and, as she gradually withdraws the abdomen from the chamber, more eggs are laid. When such a chamber is filled, she secretes a weather-proof cap to cover the opening to protect the eggs from enemies and the elements.

Many members of the subfamily Oedipodinae have brightly banded hind wings of blue, red, pink, and black. In the field, males of many of these species attract attention by the crackling noise they make in flight.

To the Locustidae belongs the interesting and important group of grasshoppers known as migratory locusts. These are species which periodically develop populations of a size which staggers the imagination. Under these conditions the locusts soon completely denude the area in which they develop and after maturity migrate in huge swarms to other areas. These swarms may travel many hundred miles, eating all the foliage and visiting complete destruction on farm crops in their path. Every continent has its particular migratory species. In North America one of the most important is *Melanoplus mexicanus*. This species swarmed through the Middle West in 1873 and 1933 (plus several years after each date). These swarms extended from the Rocky Mountains eastward to about the Mississippi River.

Several other species of grasshoppers cause serious but less spectacular damage year after year. The most persistent are other species of the genus *Melanoplus*, including *femur-rubrum*, *bivittatus*, and *differentialis* and *Camnula pellucida*. Also local non-migratory populations of *mexicanus* in the eastern part of its range cause some damage. All these species eat a wide variety of crops, and the species occurring in the western states are extremely destructive to range land following overgrazing.

Tettigidae. This contains the grouse locusts or pygmy locusts. At first glance these appear similar to short-horned grasshoppers, but

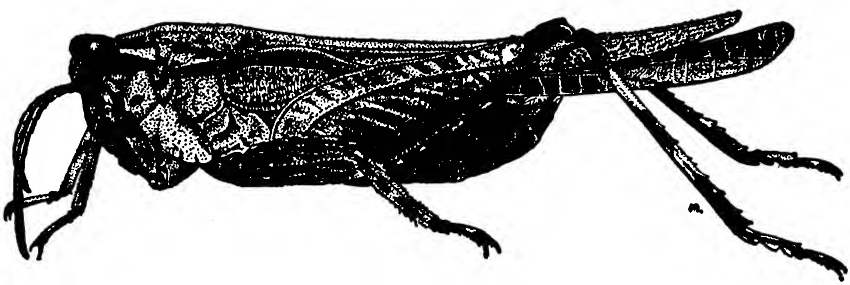

FIG. 207. A pygmy locust *Acridium ornatum*. (From Illinois Natural History Survey)

they differ from them in having the pronotum produced posteriorly into a long narrow shield extending over the entire length of the body, fig. 207. The North American species are few in number and all small, seldom more than 15 mm. long. They occur in a variety of situations, especially moist places near water. Certain species of the family display extraordinary variations in color pattern and have been employed in genetics research.

Tettigoniidae. Here belong the long-horned grasshoppers, those Saltatoria in which the antennae are long and slender, as long as or longer than the body, and the tarsi are four-segmented. The family is a large one, embracing the meadow grasshoppers, fig. 208; the cone-

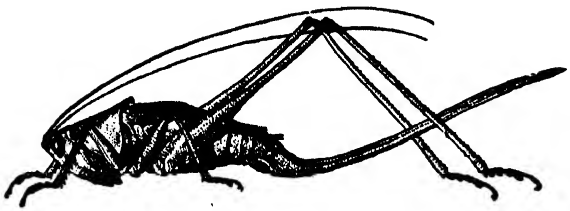

Fig. 208. A female meadow grasshopper *Conocephalus strictus.* (From Illinois Natural History Survey)

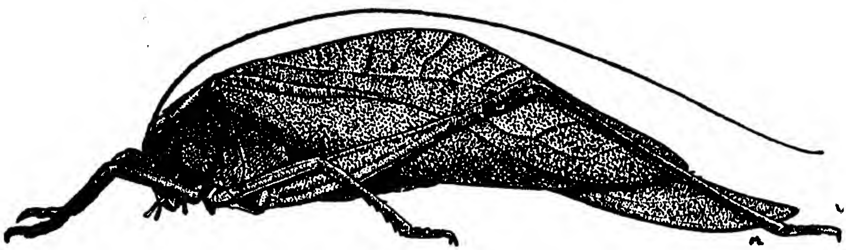

Fig. 209. The bush katydid *Microcentrum rhombifolium.* (From Illinois Natural History Survey)

Fig. 210. A camel or cave cricket *Ceuthophilus maculatus.* (From Illinois Natural History Survey)

headed grasshoppers; the various types of katydids, fig. 209; and the cave or camel crickets, fig. 210. Best known are the katydids, which are large, usually green or pinkish insects with wide wings. The

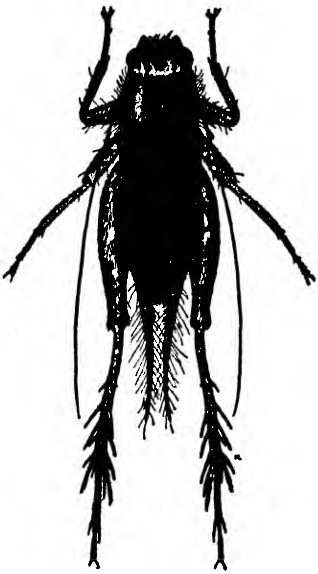

Fig. 211

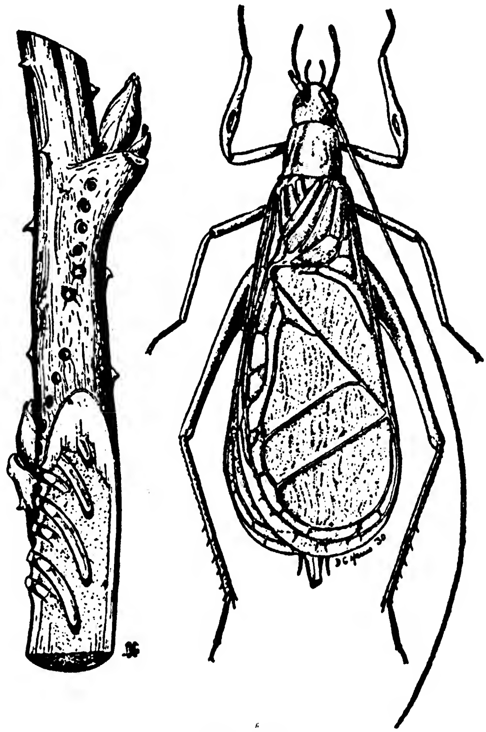

Fig. 212

Fig. 211. A field cricket *Nemobius fasciatus*. (From Illinois Natural History Survey)

Fig. 212. The snowy tree cricket *Oecanthus niveus*. Egg punctures and eggs exposed to view in a raspberry cane, and adult male. The males are among the most fascinating insect musicians. (From Essig, after Smith, "College Entomology," by permission of The Macmillan Co.)

katydids produce a musical series of chirps and as insect musicians are as renowned as the crickets.

The most destructive member of the Tettigoniidae is *Anabrus simplex*, the Mormon cricket. This is a large wingless western species which often occurs in outbreak numbers in the Great Basin region of the Rocky Mountains and inflicts great damage on natural range and cultivated grain and grass crops.

Gryllidae. A varied assemblage of crickets comprise this family; these have long antennae, as have the Tettigoniidae, but the tarsi are three-segmented. A number of genera such as *Nemobius,* fig. 211, live in open fields or in woodland grasses. Other genera frequent shrubs or trees. One of these, *Oecanthus,* containing the tree crickets,

FIG. 213. Mole cricket *Gryllotalpa hexadactyla.* (From Illinois Natural History Survey)

has an awl-shaped ovipositor with which it drills holes into pithy stems and deposits its eggs in these holes, fig 212. In local areas raspberry canes may be injured seriously in this manner by *Oecanthus* females.

The mole crickets represent two other families, the Gryllotalpidae and the Tridactylidae. The Gryllotalpidae, fig. 213, are about an

FIG. 214. Pygmy mole cricket *Tridactylus minutus.* (From Illinois Natural History Survey)

inch (25 mm.) long and have large scooplike front legs used in digging. The species make burrows in fairly light soil and feed on small roots and insects which they encounter underground. The adults rarely emerge from their burrows and are seen only occasionally. The Tridactylidae, or pygmy mole crickets, are much

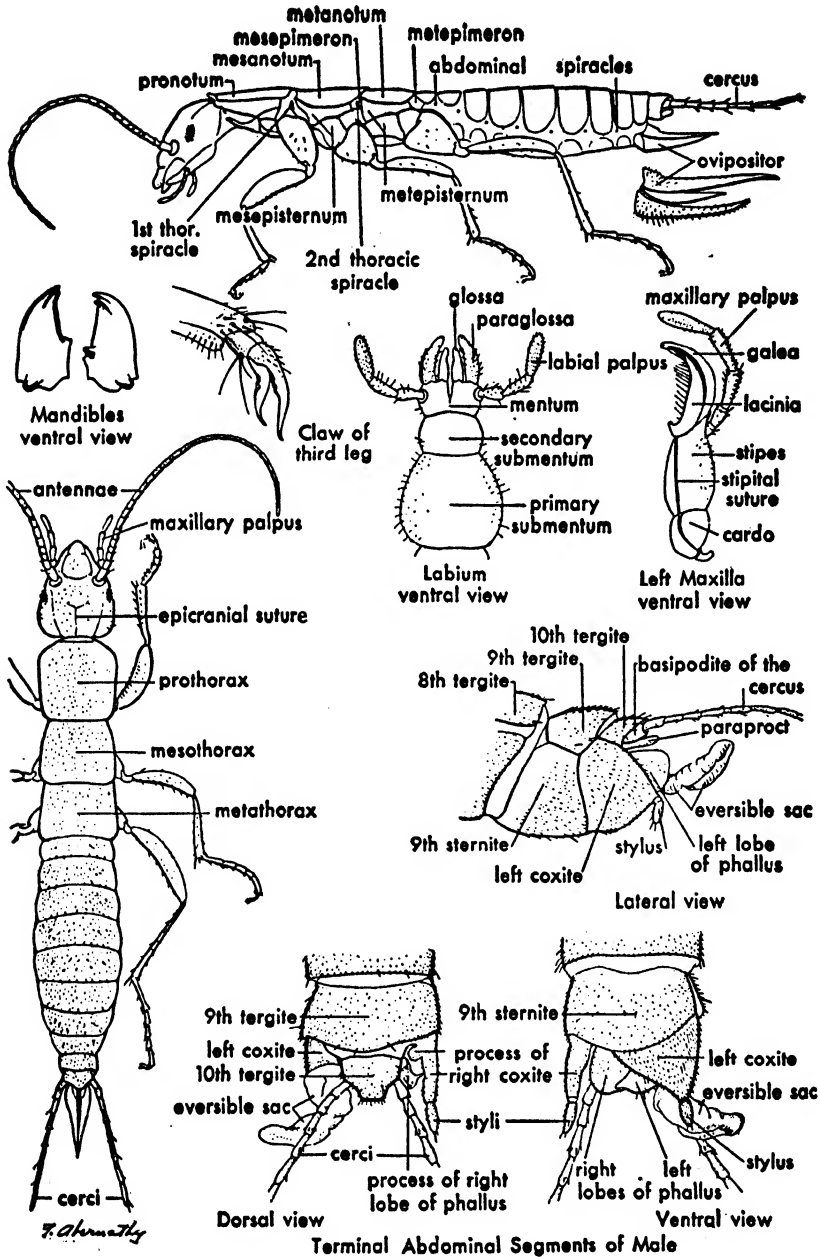

FIG. 215. *Grylloblatta campodeiformis.* (From Essig, "College Entomology," by permission of The Macmillan Co.)

smaller, at the most 5 mm. long, fig. 214. They occur at the edge of lakes and streams, where they may be found either burrowing in the sand or leaping about near the shore line.

Suborder GRYLLOBLATTODEA

The Grylloblattids

This suborder is composed of one family, the Grylloblattidae, which contains only the single genus *Grylloblatta*. These are small wingless elongate insects, fig. 215, the head bearing long antennae, small eyes, and chewing mouthparts of generalized shape. The legs are slender, but well developed, and have five-segmented tarsi. The abdomen of the female bears at its apex a stout ovipositor and in both sexes a pair of eight- or nine-segmented cerci.

These are among the most interesting of all insects. In North America they have been found near the snow line of a few mountains in western Canada, California, Montana, and Washington. They live in soil or rotten wood, or under logs or stones, always in places which are covered with snow for much of the year. They feed on vegetation or dead organic matter. The females deposit black eggs in moss or soil.

Only a very few species of grylloblattids have been described. In addition to North America they have been found in Japan.

References

See under Dermaptera.

Order DERMAPTERA

Earwigs

Medium-sized elongate heavily sclerotized insects in which the abdomen has a pair of stout forceps, the modified cerci, fig. 216. The mouthparts are a simple chewing type; the compound eyes are large, the ocelli usually indistinct or lacking; the antennae are long, multisegmented, and slender. Wings are sometimes lacking; if present, the first pair forms short usually truncate veinless hard wing covers, and the second pair is fan-shaped, with a peculiar radial venation, fig. 217. When not in flight, the second pair folds into a complicated compact mass almost entirely covered by the wing covers or elytra. Metamorphosis is gradual.

The earwigs in North America vary from about 5 to 15 mm. in length but are otherwise relatively uniform in shape and habits. They are nocturnal, roaming actively at night, and are omnivorous in food habits. Some species are apparently predaceous; others feed chiefly on decayed vegetation, or occasionally on living plant tissue. During the day they hide in a wide variety of tight places—under bark and boards, in the soil, and in cracks and crevices of every sort.

FIG. 216. An earwig *Labia minor.* (From Illinois Natural History Survey)

The life history of earwigs is simple. The female lays a large cluster of white ovate eggs in a chamber in the ground in some protected spot. She watches over these for the few days required for hatching, and then extends her maternal care over the young for at least a short period, fig. 183. The young pass through four to six molts, maturing fairly rapidly. In temperate regions there is only one generation a year.

The group is chiefly tropical, with a few representatives extending north into temperate areas. Less than twenty species occur in America north of Mexico, representing two families and several genera. The most widely distributed is the small *Labia minor* which is an introduced species, as are most of the nearctic earwigs.

Economic Status. In certain areas of North America the cosmopolitan European earwig *Forficula auricularia* has become a pest of great importance. It is especially abundant on the West Coast, where it is destructive to roses, dahlias, and other flowers, eating off the petals at the base and causing them to drop. Aside from this habit, it is chiefly a general feeder around the garden and home. Community poison-bait campaigns are often carried out in efforts to reduce its numbers.

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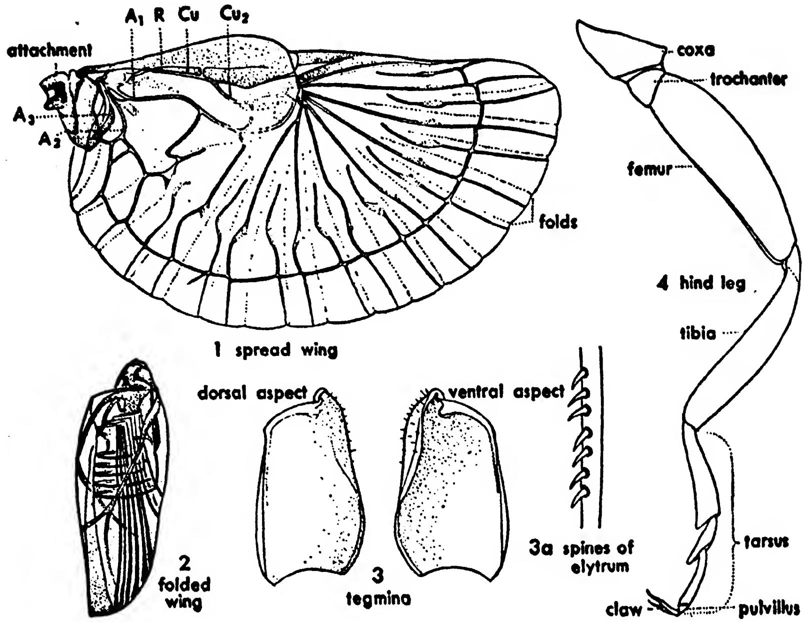


Fig. 217. Structures of an adult earwig. (From Essig, "College Entomology," by permission of The Macmillan Co.)

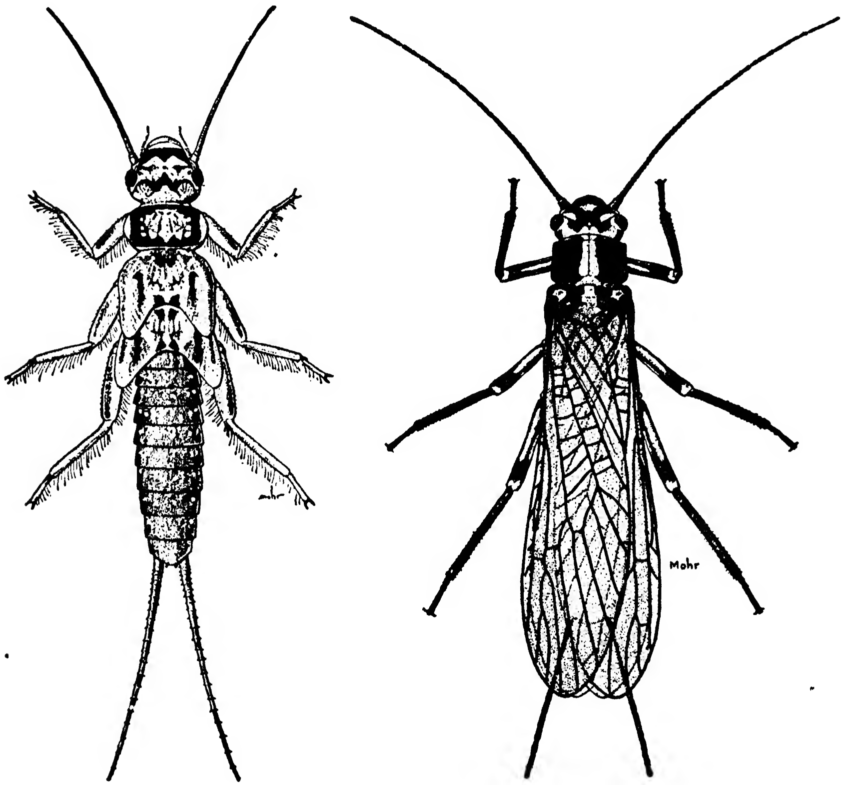
Order PLECOPTERA

Stoneflies

Moderate-sized to large insects with aquatic nymphs and gradual metamorphosis. The adults, fig. 218, have chewing mouthparts, frequently reduced in size and sclerotization; long many-segmented antennae; distinct eyes and ocelli; cerci ranging from short and one-segmented in some families to long and multisegmented in others. Two pairs of well-developed wings are almost always present. These are of similar texture and have only a moderate number of veins but frequently a large number of crossveins; the front pair is usually narrower than the hind pair. Several species have short wings, and in *Allocapnia vivipara* the males have no wings. The nymphs, fig. 218, of all stoneflies are aquatic. They have long antennae and a pair of long multisegmented cerci, chewing-type mouthparts, well-developed eyes and ocelli, and body proportions as in adults.

The nearctic stoneflies include about two hundred and fifty species, comprising about ten families and thirty-five genera. Their generalized mouthparts, antennae, and wings, together with their simple type of metamorphosis, indicate that the order is a primitive one allied to the Orthoptera.

The nymphs of this order are one of the abundant and interesting components of stream life. They range in body length from about



Nymph Adult

FIG. 218. A stonefly *Isoperla confusa,* nymph and adult. (From Illinois Natural History Survey)

5 to over 20 mm. and present a varied appearance, including drab plain forms, spotted patterns, and forms striped with yellow, brown, or black. Many of them breathe by means of external finger-like gills. Sometimes the gills are filamentous. The gills are single in some and arranged in tufts in others. Some nymphs have no external gills and simply use the cuticle for respiration. As a rule, the nymphs are found in cool unpolluted streams; a few species occur also along the wave-washed shore area of some of the colder lakes. The nymphs live in a variety of situations, frequently specific for the species. They

are found under stones, in cracks of submerged logs, in masses of leaves which accumulate against stones or around branches trailing in the water, and in mats of debris. The majority of the nymphs are vegetarian, feeding on dead organic matter presumably incrusted with algae and diatoms. A number of species are predaceous, feeding on small insects and other aquatic invertebrates.

The females lay several hundred to several thousand eggs, discharging them in masses into the water. The eggs soon hatch. The smaller species and some large ones mature in 1 year, but other large species require 2 years to complete their development. When full grown, the nymphs crawl out of the water and take a firm hold on a stone, stick, tree trunk, or other object preparatory to the final molt. At molting a dorsal split occurs in the nymphal skin; then the adult emerges in about a minute or less. After another few minutes the wings have expanded and hardened enough for flight. The adults live for several weeks.

There is a peculiarity about certain groups of stoneflies which is only rarely encountered among insects. Winter signals the end of the active season and the beginning of the quiescent period for most insects. With many of the stoneflies the opposite is the case. Apparently the first-instar nymphs do not develop further during the warmer months of the year. With the approach of winter, nymphal development becomes accelerated, and the adults emerge during the coldest months of the year, beginning in late November or early December, and continuing through March. The adults are active on the warmer winter days and may be found crawling over stones and tree trunks, mating, and feeding on green algae. They show a decided preference for concrete bridges and may be collected in great numbers there. This group is called the fall and winter stoneflies and includes roughly the families Capniidae, Leuctridae, Nemouridae, and Taeniopterygidae. The latter three have members which appear later in the year, and their emergence overlaps that of the spring and summer species.

This peculiar growth behavior of the fall and winter stoneflies indicates a physiological adjustment to the warm and cold seasons quite different from that in most insects. When discovered, the controls and mechanisms for this adjustment will make an interesting story.

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Order ISOPTERA

Termites, White Ants

Termites are medium-sized insects having gradual metamorphosis, living in large colonies much like those of ants, and having several different social castes. A typical colony, for example, has three castes: sterile workers, sterile soldiers, and sexual forms (reproductives), figs. 219, 220. The workers are white and sometimes appear translucent. They are wingless, and have round heads, long antennae, chewing mouthparts, and small eyes or none at all. The legs are well developed and all about equal in size. The soldiers have bodies similar to those of the workers, but their heads are enlarged and have massive mandibles. The reproductives are of two types: One type is white, wingless or with only short wing pads; the other type includes fully formed sclerotized winged males and females. These, fig. 220, have round heads, long antennae, chewing mouthparts, well-developed eyes, and two pairs of similar transparent wings. After mating and dispersal flights, the wings fall off, each one leaving only a short stub or scale which persists for the life of the individual.

The termites in North America feed on cellulose, in almost all cases obtained from dead wood. The colonies, which may number several thousand individuals, are located in dead trees or logs or in the ground with covered runways connecting the nest to a log or stump which provides a food supply. The workers do all the foraging for the colony, feeding both the soldiers and reproductives. The soldiers afford protection from enemies from the outside, taking up strategic stations near the exits of the colony. The reproductives are the only fertile members of the colony and produce eggs almost continuously. The workers take care of the eggs until they hatch.

During most of the year only workers and soldiers are produced, but once a year, in spring or fall, a brood of winged males and females is produced by the more northern species. These are fully formed reproductive individuals called the *first reproductive caste.* They leave the nest in swarms, disperse, mate, and form new colonies.

A new colony is established by a single pair of winged individuals. The male and female lose their wings after the dispersal flight and, in our species, together eat out a small nest in a dead stump or log. They feed as normal individuals, and the female produces eggs which

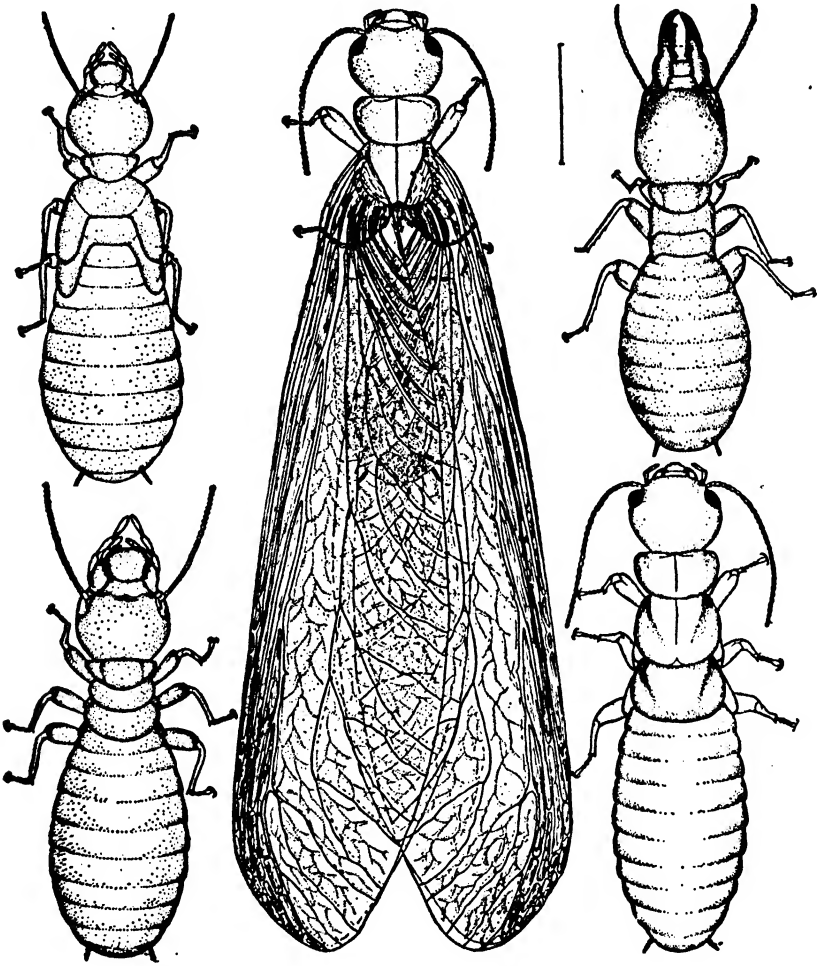

FIG. 219. Castes in a colony of termites, order Isoptera. Center, first form or winged reproductive; upper left, second form reproductive; upper right, soldier; lower left, worker; lower right, first stage reproductive after the wings have broken off. (From Duncan and Pickwell, "A World of Insects," by permission of McGraw-Hill Book Co.)

develop into workers and soldiers. When a sufficient number of these have matured, these neuter castes take over the activities of nest expansion and the feeding of both the female and male, called the *queen* and *king* of the colony. If either of these die, their place is taken by the worker-like fertile forms known as the *second reproductive caste.* These are produced in small numbers in most colonies and appear to be held in reserve for substitution purposes.

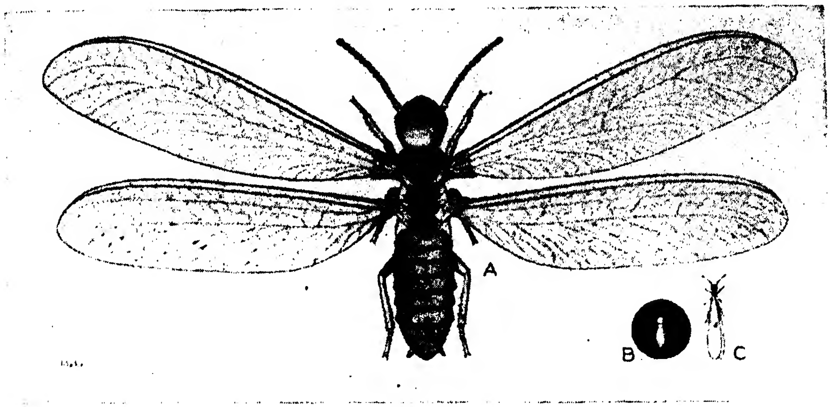

Fig. 220. Sexual winged form of a termite *Reticulitermes flavipes,* greatly enlarged. In *B* is a worker and in *C* a winged form, natural size. (From Illinois Natural History Survey)

In certain genera of North American termites there are no soldiers, but instead a caste called *nasutes,* fig. 221. These have a curious snoutlike head; they produce a droplet of liquid with high deterrent quality and use it to repel enemies of the colony.

Economic Status. Every year termites cause a large loss to buildings and libraries. In their search for cellulose, several kinds of termites invade foundation woodwork of buildings and may spread from that point through the woodwork into upper parts of buildings. They may cross masonry or metal in their progress. Over these non-wood areas they build covered runways out of excrement, soil, and chewed wood and by this means always keep a contact with the soil from which they derive needed moisture. Books or wooden furniture may be attacked if these are stationary for long periods and in contact with wood. Freak cases of termite attack like the following are not uncommon. In an Urbana, Ill., high school of concrete construction, an instructor was leaning against a corner of the desk. Suddenly there was a grinding of wood and the desk

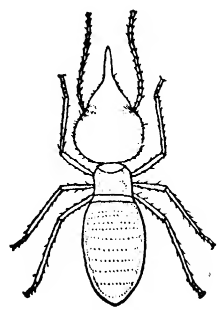

Fig. 221. Nasute of a termite. (Adapted from Banks and Snyder)

literally fell apart and crumbled to pieces. Out of the wreckage cascaded thousands of termites, which had eaten away the inner portions of the wood, never breaking through the wood surface but excavating the softer inner-ring fiber of every board. How the termites reached the desk appeared a mystery. Investigation finally showed that they had entered a piece of wood bracing embedded in the concrete foundation. This led from the ground to the next floor, which was of oak. The desk rested squarely on the oak floor. Along this unseen but direct route the termites had eaten their way, undetected until the desk was so thoroughly eaten away that a chance pressure caused it to break.

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Order ZORAPTERA

Zorapterons

Minute insects, 1.5 to 2.5 mm. long, with both winged and wingless adult forms, fig. 222. In both the head is distinct and oval and has chewing-type mouthparts, long nine-segmented antennae, and one-segmented cerci. The wingless forms are blind, with only occasional vestiges of eyes or ocelli; the winged forms, or alates, have compound eyes and distinct ocelli. The alates have two pairs of delicate membranous wings, each with only one or two veins which may be branched. These wings are shed by the adults much as in the termites, leaving only small stubs attached to the body. Metamorphosis is gradual.

The order is one of the rarest among the insects. It contains one family, the Zorotypidae, in which there is only a single genus, *Zorotypus*. From the entire world less than twenty species are known, most of them found in the tropics. Two occur in North America, *Z. snyderi* described from Jamaica and Florida, and *Z. hubbardi* which has been collected in many localities in the southern states as far north as Washington, D. C.

Extremely little is known of the bionomics of these interesting creatures, and most of this information has been obtained from studies

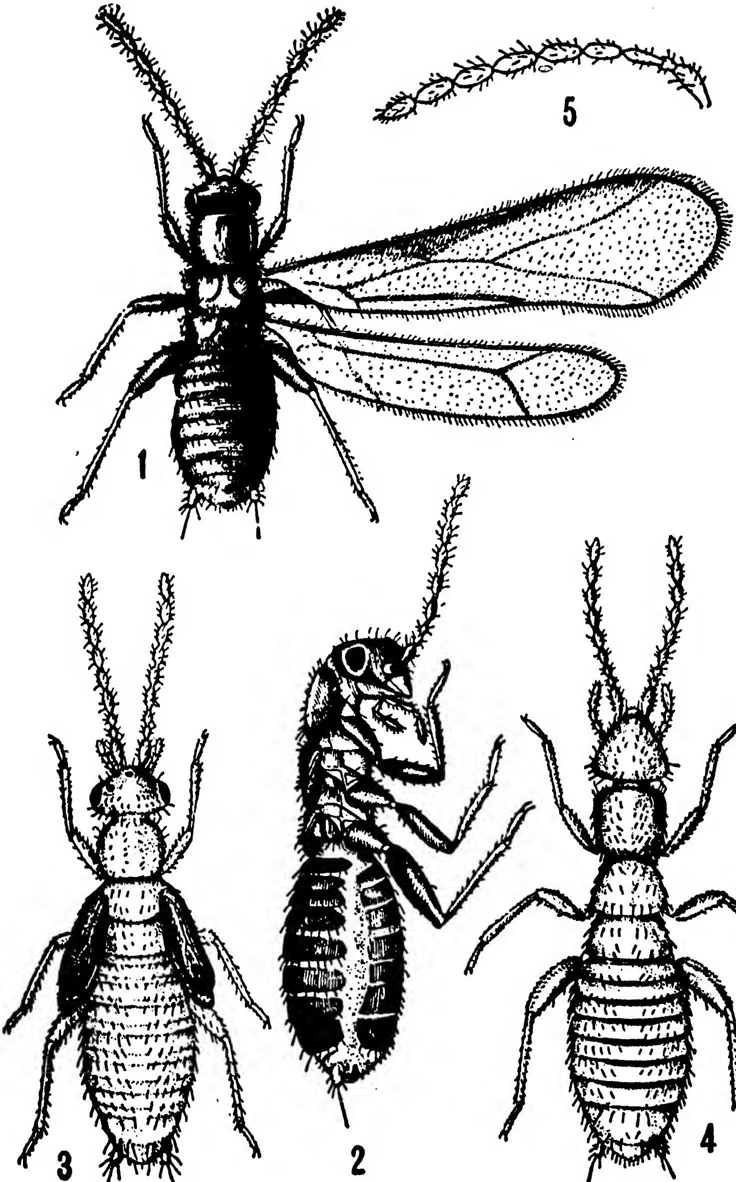

FIG. 222. Forms of *Zorotypus hubbardi.* 1, winged adult female; 2, adult female that had shed her wings; 3, nymph of winged form; 4, wingless adult female; 5, antenna of adult wingless *Zorotypus snyderi.* (After Caudell)

of *Zorotypus hubbardi*. Gurney (1940) has summarized previous observations on the order and contributed much additional information based on his own studies.

Zorapterons live in rotten wood or under dead bark and are usually found in colonies of less than twenty-five individuals, although occasionally a colony may have as many as one hundred members. Their food, as far as is known, consists mainly of small arthropods, especially mites and small insects. This has been deduced from an examination of stomach contents, which have included pieces of sclerites permitting partial identification of the food. Whether they are scavengers or predators has not been established, but observations on culture specimens indicate the former.

The wingless and winged adults have similar genitalia and reproductive habits. Eggs of only *Z. hubbardi* have been observed. They were laid in the runways of the colony, without definite anchor lines or matrix. The creamy-colored oval eggs hatched in about 3 weeks. Basing his estimate on collection observations over several years, Dr. Gurney believes that it requires several months for the nymphs to become adults.

Although the development of winged and wingless forms might indicate a forerunner of a caste system, no evidence of social life has been observed in the Zoraptera. There is apparently no division of labor, care of young, or social interrelationship between individuals. The gregarious nature of the colonies is very similar to the conditions found in many species of Corrodentia.

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Order EMBIOPTERA

Embiids, Web Spinners

Elongate flattened insects, fig. 223, with curious enlarged front tarsi, used for spinning silken webs. Mouthparts are the chewing type, primitive in structure; eyes well developed, ocelli absent; antennae many-segmented and elongate; legs short but stout, the tarsi three-segmented; cerci one- or two-segmented. Females always wingless; males

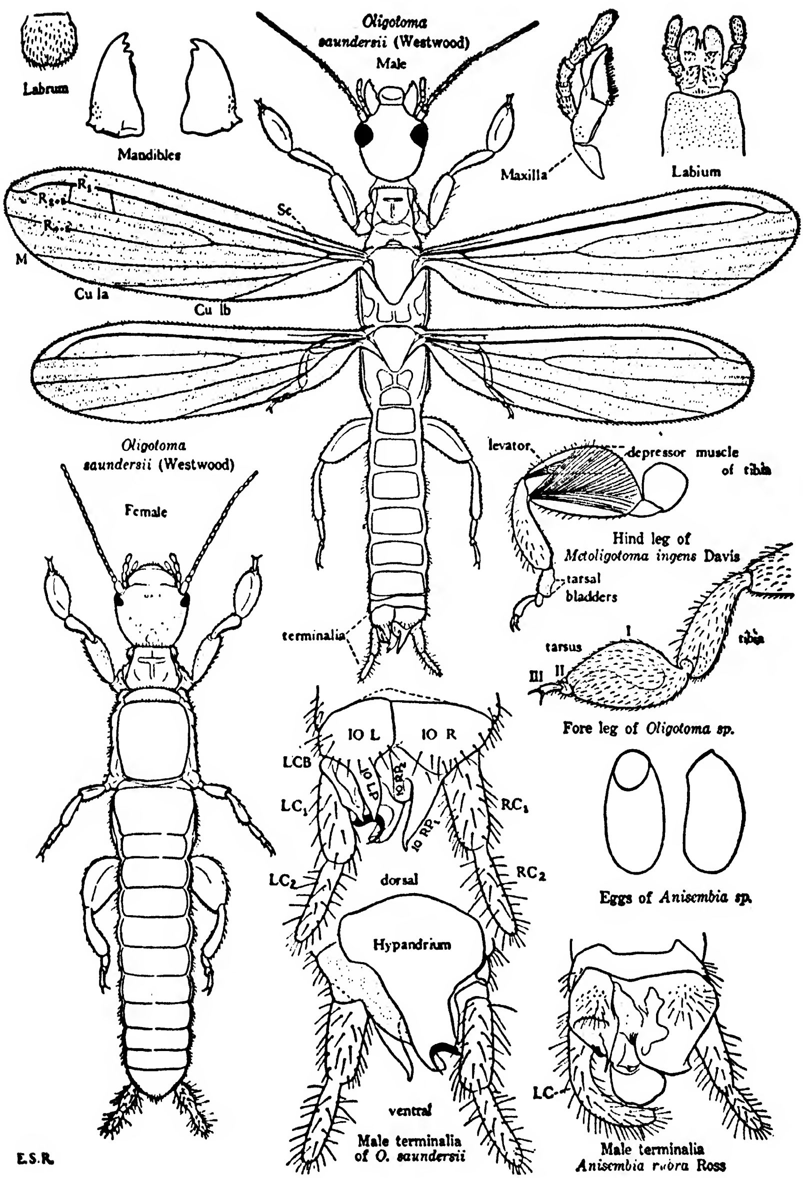

FIG. 223. Structures and forms of Embioptera. Letters on male terminalia refer to special parts used in embiid taxonomy. (From Essig, "College Entomology," by permission of The Macmillan Co.)

usually with two pairs of long membranous similar wings with reduced venation. Metamorphosis gradual.

To this order belong a small number of peculiar tropical and semitropical insects, which live in silken tunnels on their food supply. They feed on a wide variety of plant materials, especially dried grass leaves. Their tunnels may be found under loose bark, among lichens, or on the ground. The ground nets are often among matted leaves, or under dry cattle droppings or stones. Sometimes these nets are found around the bases of plants. In arid regions the insects may be active at the ground surface during the wet seasons and retire into the soil during the dry season. The embiids themselves are active and rapid in movement. The winged males fly readily and are frequently attracted to lights.

The web spinners live in large colonies, with numerous interlocking tunnels, and are gregarious. Most species have both males and females, but a few are parthenogenetic, and of these only females are known. The eggs are elongate and relatively large. They are laid in clusters attached to the walls of the tunnels. The female exhibits considerable maternal interest in both eggs and newly hatched nymphs, remaining near them and attempting to drive away enemies.

The nymphs are remarkably similar to the adults that are wingless. In those species with winged males, there is a noteworthy phenomenon. In the male nymphs the wing pads develop internally as imaginal buds until the penultimate molt and appear as typical wing pads only in the last nymphal instar. This is what happens in holometabolous insects, so that this last embiid nymphal stage might well be called a pupa.

About seventy species of the order have been found in the Americas, representing seventeen genera and six families. Most of these occur in the tropical areas, but five species extend north into the southern portion of California, Arizona, Texas, and Florida. Two of these, *Oligotoma saundersii* and *nigra,* are tropicopolitan, and have been transported by commerce to most of the equatorial world. A few additional species are occasionally found by quarantine inspectors in shipments of material to the United States from other countries.

All species of the order are remarkably uniform in general appearance. In fact, to date few characters have been discovered to use for the identification of the females, and almost the entire classification of families, genera, and species is based on males.

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Order CORRODENTIA

Psocids, Booklice

Small insects, ranging in length from 1.5 to about 5 mm., with chewing mouthparts, long 13- to 50-segmented antennae, small prothorax, and no projecting cerci, fig. 224. Two pairs of wings are well developed in some forms, the front pair much larger than the hind pair, both of similar texture and with a reduced and simple venation. In other forms the wings may be small and scalelike or absent. Metamorphosis is gradual.

Most of the members of this order are small, averaging 2 to 4 mm. in length, and are either inconspicuously colored or exhibit marked protective coloration. For this reason they are seldom collected by the beginning student, although they occur abundantly in many habitats. Their food is relatively non-specific, consisting of fungus mycelium, lichens, dead plant tissue, and dead insects, even of their own species. They live in a wide variety of situations out-of-doors—on clumps of dead leaves, dried standing grass, dead or dying leaves of corn plants, bark of tree trunks, in the leaf cover on top of the ground, on shaded rock outcrops, under fence posts, and in bird and rodent nests. Several species live on moldy or partially moldy foods, bookbindings, and almost anything with available starch or fungus mycelium.

Some of the species are stocky and move slowly, even when disturbed. Many of them are more slender, and a few are quite flat. These usually move with considerable speed, and a few are among the most rapid dodgers to be found among the insects. Studies to date indicate that the entire life span from egg to death of the adult is between 30 and 60 days, of which about half is spent in the adult stage. The eggs are laid on the leaf surface or other spot which the adult frequents. Depending on the species, eggs are deposited singly or in groups up to about 10. After oviposition the female spins strands of silk over the eggs and anchors them to the surface of the support. In some species only a few strands are spun over the eggs; in others

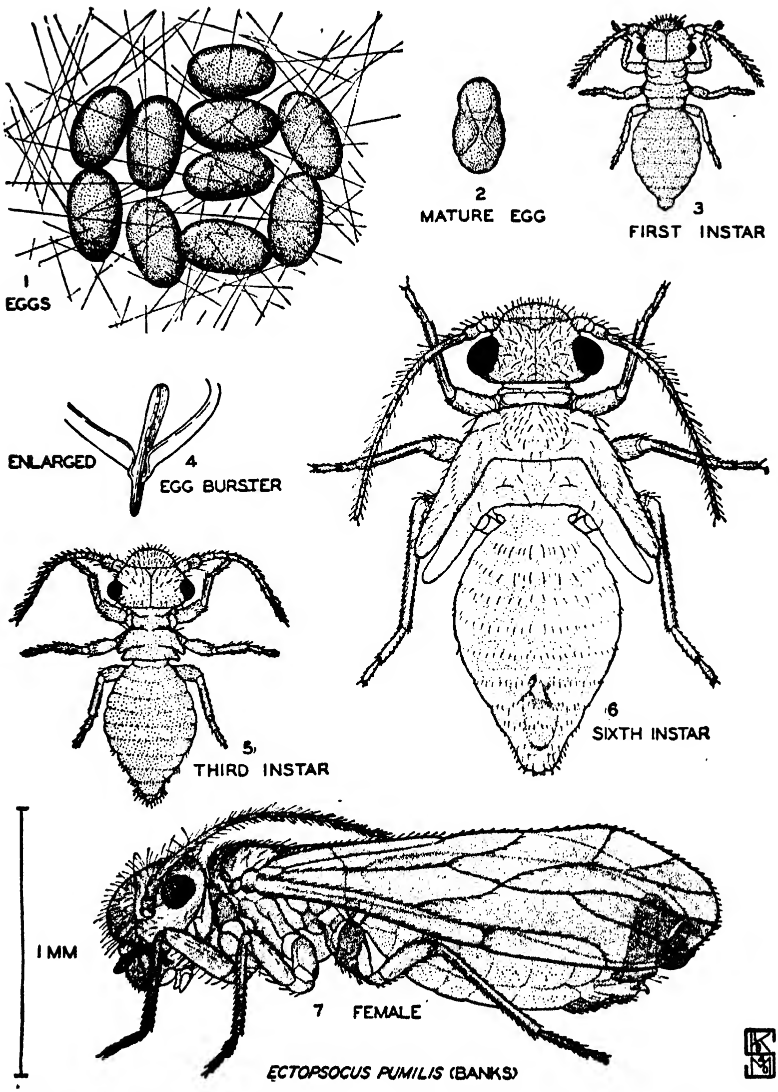

Fig. 224. A winged psocid *Ectopsocus pumilis,* and its life history stages. (After Sommerman)

a dense web may be spun over each group of eggs. The eggs hatch in a few days, and the nymphs pass through six nymphal stages and become adults in 3 or 4 weeks.

In the more northern states the winter is passed in the egg stage by some species and as nymphs or adults by others. Species inhabiting warm buildings continue to breed throughout the year.

About one hundred and fifty species are known from North America, representing about six families and many genera. The group is world-wide in distribution, with an estimated number of species nearing nine hundred.

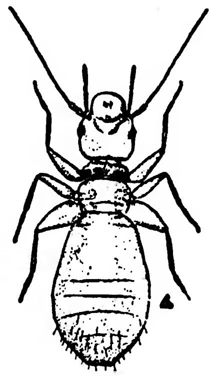

Fig. 225. A wingless book louse *Liposcelis divinatorius*. (From U.S.D.A., B.E.P.Q.)

Economic Status. Several species of psocids cause considerable waste of food and damage to libraries. They cause little loss by actually eating foodstuffs, because they feed chiefly on mold. At times, however, they become extremely abundant, spread through an entire building, and get into every possible hiding place. In this way they may contaminate otherwise merchantable goods to such an extent that quantities of the material must be discarded. Their damage to libraries is more direct. They eat the starch sizing in the bindings of books and along the edges of the pages, defacing titles and necessitating rebinding and repairs. The two most common species are the common book louse, *Liposcelis divinatorius*, a minute wingless species, fig. 225; and *Trogium pulsatorium*, another small species having the wings reduced to small scales.

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Order MALLOPHAGA

Bird Lice, Chewing Lice

Small to medium-sized wingless insects, usually flattened, fig. 226, which live as ectoparasites on birds and mammals. They have chewing mouthparts; only short three- to five-segmented antennae, sometimes hidden in a recess of the head; reduced compound eyes; and no ocelli. The thorax is small; the legs short but stout, fitted for running; the abdomen has no cerci.

The chewing lice average about 3 mm. in length, a few species attaining 10 mm. They vary considerably in shape and habits, some being long and slender, others short and wide; some are active and

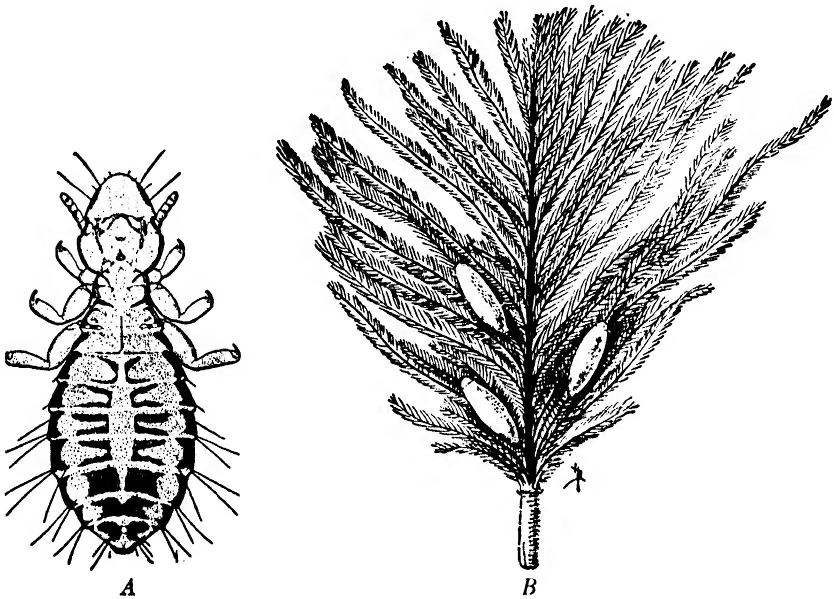

FIG. 226. The chicken head louse *Cuclotogaster heterographus*. *A*, adult; *B*, eggs on feather. (*A*, from Illinois Natural History Survey; *B*, from U.S.D.A., B.E.P.Q.)

rapid of movement, others sedentary and sluggish. There is little correlation between speed and shape. Their mouthparts are of the chewing type, but greatly reduced and difficult to interpret without careful study.

There are several hundred species of Mallophaga in North America, comprising about six families and many genera. The various species occur on only one species of host, or on a group of closely related species. The turkey louse, for instance, occurs only on turkeys, but the large poultry louse occurs on many kinds of domestic fowl, such as chickens, turkeys, peacocks, guinea hens, and pigeons. The small family Trichodectidae occurs only on mammals, and the large family Menoponidae occurs only on birds.

All the Mallophaga live entirely on the host body and have continuous and overlapping generations throughout the year. They feed on scaly skin, bits of feather, hair-clotted blood, and surface debris. The eggs are glued to the hair or feathers of the host and thus kept under incubator conditions. The eggs of various species differ in shape; some are long and simple, as in fig. 226*B;* others are ornamented with tufts of barbs or hair, as in fig. 227*B*.

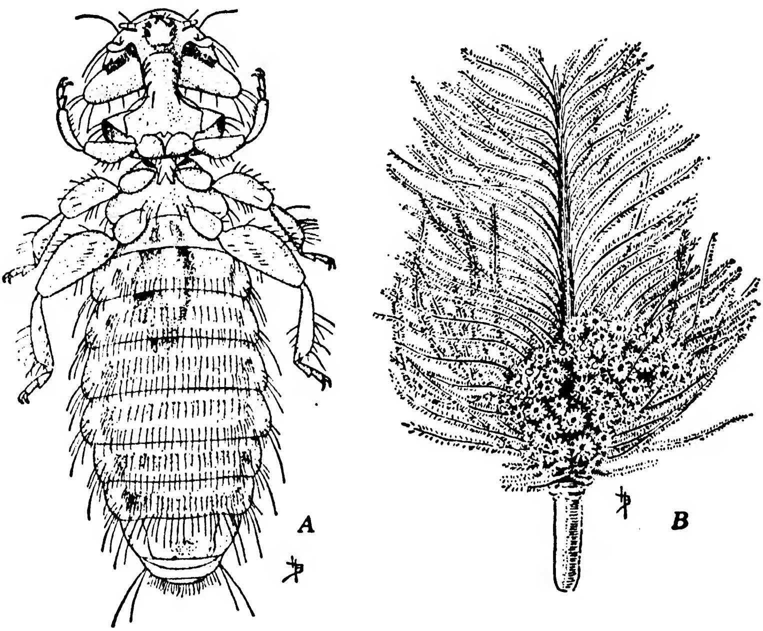

FIG. 227. The chicken body louse *Eomenacanthus stramineus*. *A*, adult; *B*, eggs on feather. (From U.S.D.A., B.E.P.Q.)

Economic Status. Many species of Mallophaga infest domestic birds and animals and cause a considerable over-all loss. Poultry are the most important group attacked. Chicken lice, *Menopon gallinae* and *Eomenacanthus stramineus,* fig. 227, cause loss of weight and reduction of egg laying in chickens, turkeys, and other fowl. The chicken-head louse *Cuclotogaster heterographus,* fig. 226, occasionally occurs in outbreak form and causes the death of broods of young chicks. Several other species infest fowl, but the afore-mentioned, because of their reproductive capacity, are the most common and destructive.

Domestic animals are attacked by various species of the genus *Trichodectes*. Dogs, cats, horses, cattle, sheep, and goats may suffer considerable loss of condition if badly infested with these lice. There is evidence that the biting sheep louse *T. ovis* injures the base of the wool and causes commercial depreciation by lowering the staple length of the sheared product.

Reference

Ewing, H. E., 1929. Mallophaga, or biting lice. A manual of external parasites, pp. 90–126, figs. 58–70. Baltimore, Thomas.

Order THYSANOPTERA

Thrips

Small elongate insects, fig. 229, most of them between 2 and 3 mm. long, with six- to nine-segmented antennae, large compound eyes, and compact mouthparts which form a lacerating–sucking cone. Many forms are wingless; others may have short wings or well-developed wings. In the latter case there are two pairs, both very long and narrow, with only one or two veins or none; the front pair often larger, and both with a long fringe of fine hair along at least the hind margin. The legs are stout, the tarsi ending in a blunt tip containing an eversible pad or bladder. Metamorphosis is gradual, but there is present an incipient pupa.

The thrips are an extremely interesting group, quite different from any related forms. They occur commonly in flowers, and they may be found by breaking open almost any blossom and looking around the bases of the stamens or pistils. A large number of diverse forms can be taken by sweeping grasses or sedges in bloom. Many species are destructive to various plants and are found on the leaves of infested hosts. A large number of species, predaceous on mites and small insects, occur under bark of dead trees and in ground cover.

Thrips' mouthparts are of an unusual type, fig. 228. The various parts fit together to form a cone; some of the parts are needle-like stylets, which pierce and lacerate the food tissues; the juices thus released are sucked up into the stomach by a pump in the head capsule which pulls the liquid food through the cone formed by the mouthparts.

The metamorphosis of thrips is as unusual as their morphological features. The early nymphal stages are similar to the adults in structure of legs and mouthparts and in general shape; their feeding habits are also the same as those of the adults. These points are characteristic of the hemimetabolous type of metamorphosis. The first two instars have no wing pads, fig. 229,2; the pads appear suddenly in the third instar as fairly large structures, fig. 229,3; in the fourth (last) nymphal instar the wing pads are greatly enlarged, fig. 229,4. This fourth instar is quite unlike the others in habits. It

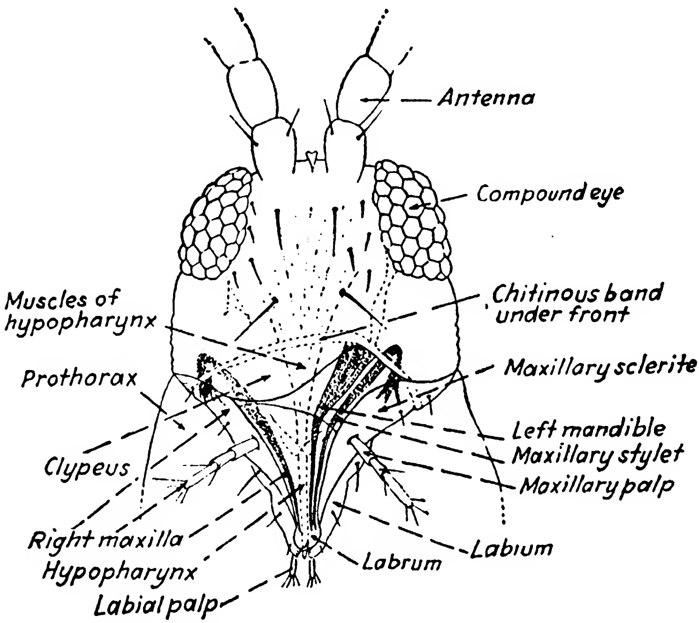

FIG. 228. Mouthparts of the flower thrips. (From Metcalf and Flint, "Destructive and Useful Insects," by permission of McGraw-Hill Book Co.)

does no feeding and is completely quiescent, with the antennae held back over the top of the head and pronotum. Certain thrips have an additional fifth nymphal instar. In some species having this, the fourth-instar nymph enters the soil and forms a cocoon, in which the quiescent fifth stage is passed. This feature is similar in so many respects to holometabolous development that the quiescent stage is called a *pupa*, and the first two instars are called larvae. The third-stage form, the active stage with the wing pads, is called a *propupa*. In some groups this form is not developed, the larvae transforming directly to the quiescent pupae.

The order contains several families represented in North America by about five hundred species, some of them measuring 5 or 6 mm.

in length. A large number of species occur on only one species of plant, but a few common species, such as the flower thrips, *Frankliniella tritici,* feed on a great variety of plants and frequent blossoms

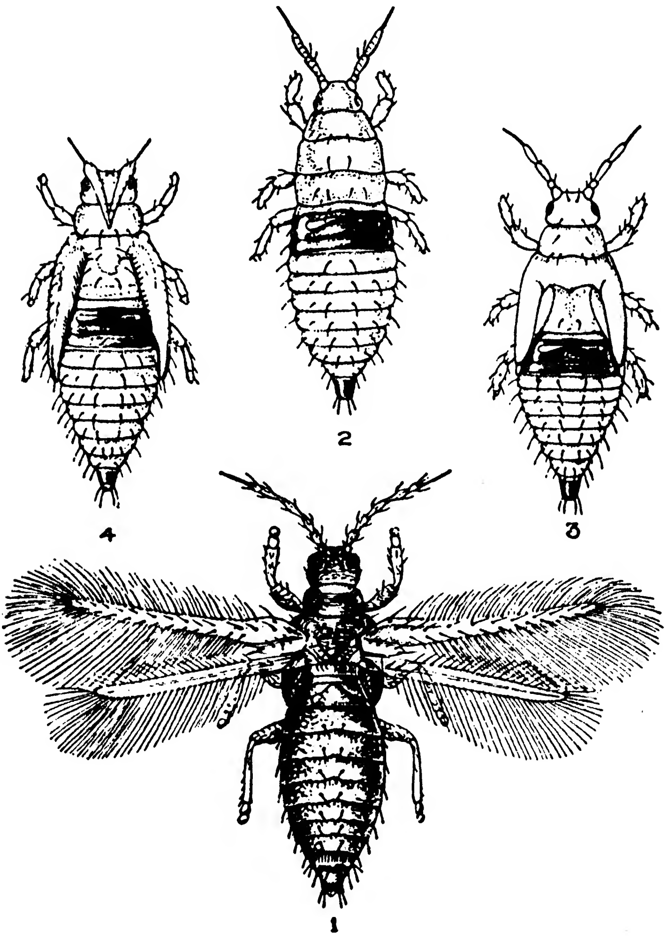

FIG. 229. The red banded thrips *Heliothrips rubrocinctus.* 1, adult; 2, nymph or larva; 3, propupa; 4, pupa. (After U.S.D.A., B.E.P.Q.)

of almost any species of plant. A few species are predaceous, feeding on red spiders and other mites, and minute insects.

Economic Status. Several species of this order inflict considerable damage on commercial crops. The following are among the most injurious thrips over the United States as a whole:

The onion or tobacco thrips *Thrips tabaci* is a widespread species varying from lemon yellow to dark brown, which is especially injurious to onions, beans, and tobacco.

The greenhouse thrips *Heliothrips haemorrhoidalis* is a dark species with the body ridged to give it a checked or reticulate surface. The species is cosmopolitan. In the temperate region it is chiefly a greenhouse pest, attacking many kinds of hothouse plants.

The pear thrips *Taeniothrips inconsequens* is brown with gray wings. It attacks pears, plums, and related plants and produces a curious silvery blistered appearance on the injured leaves.

Reference

WATSON, J. R., 1923. Synopsis and catalogue of the Thysanoptera of North America, U. Fla. Agr. Exp. Sta. Bull. **168**:1–100, bibl.

Order ANOPLURA

Sucking Lice

Wingless sluggish insects which are frequently flattened, fig. 231. They live as ectoparasites on the bodies of mammals. The mouthparts are modified to form a retractile piercing–sucking organ composed of several fine stylets whose homologies are uncertain, fig. 230. The antennae are short, three- to five-segmented; at least some legs

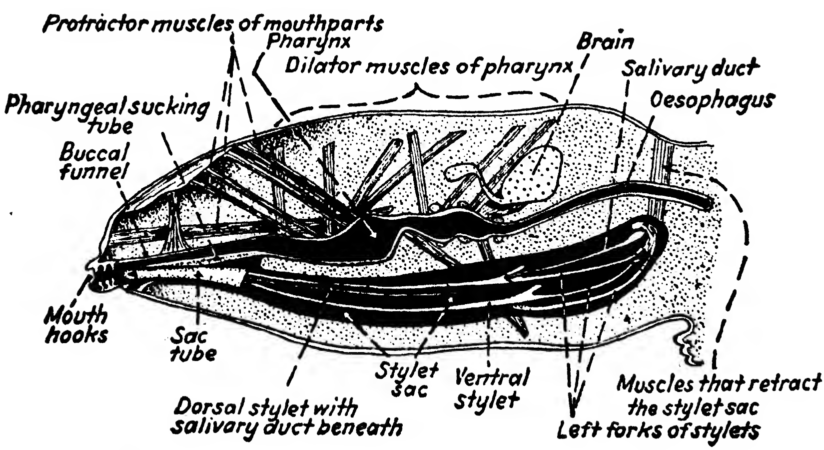

FIG. 230. Head and mouthparts of *Pediculus humanus*. (After Metcalf and Flint, "Destructive and Useful Insects," by permission of McGraw-Hill Book Co.)

end in large hooked claws; the thorax is fused into a single segment; and the abdomen has only five or eight distinct segments. Metamorphosis is gradual.

The North American species represent about twenty genera and one hundred species ranging in length from 2 to 5 mm. All of them occur normally on mammalian hosts and feed on blood. Occasionally poultry may have a small infestation of sucking lice, but all cases on record have been accidental colonizations by a common mammalian species. The entire life cycle is spent on the host. The eggs are glued to a hair and soon hatch into nymphs which are very similar to the adults in both appearance and habits. Breeding occurs continuously throughout the year.

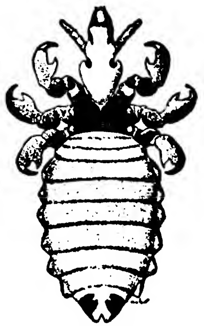

FIG. 231. The blood-sucking horse louse *Haematopinus asini*. (From Illinois Natural History Survey)

Economic Status. Sucking lice are a real concern on two counts: (1) losses inflicted on livestock, and (2) their menace to man.

Losses to Livestock. Horses, cattle, sheep, goats, dogs, and cats are attacked by several species of lice. The loss is due partly to irritation and partly to loss of blood, with resultant poor condition of the animal and failure to gain weight normally. Frequently lice will cause sheep and goats to rub against fences or trees, with heavy damage to the wool. In the main, poorly kept animals are the principal individuals badly attacked, but this is not always the case. An outbreak allowed to go unchecked will usually spread through an entire herd. Most of the lice attacking domestic animals belong to the family Haematopinidae, of which *Haematopinus asini* the horse-sucking louse, fig. 231, is a common example.

Menace to Man. Two species of Anoplura are external parasites of man. They are both widespread in distribution and are most abundant under crowded unsanitary conditions. They spread from person to person in crowded situations or by clothing and bedding.

Crab Louse, Phthirius pubis, Fig. 232. A very small crablike species infesting hairy portions of the body, especially the pubic region. It is seldom found on the head. This species inflicts painful bites and causes severe irritation. It has not been incriminated in the dispersal of any disease.

Body Louse or Cootie, Pediculus humanus, Fig. 233. A larger louse about 4 or 5 mm. long, which occurs on the hairy parts of the body. There are two forms of this species, the head louse which occurs chiefly on the head and glues its eggs to the head hairs, and the body louse which occurs chiefly on the clothes and reaches to the adjacent body areas to feed. The body louse glues its eggs to strands of the clothing. Under condition of regular head washing and clothes change cooties are seldom a nuisance. Under unsanitary conditions they may develop in tremendous numbers and produce constant irritation.

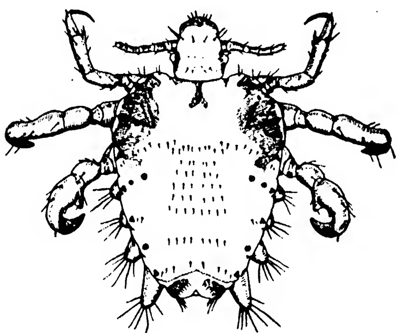

FIG. 232. The crab louse *Phthirius pubis*. (Redrawn from Ferris)

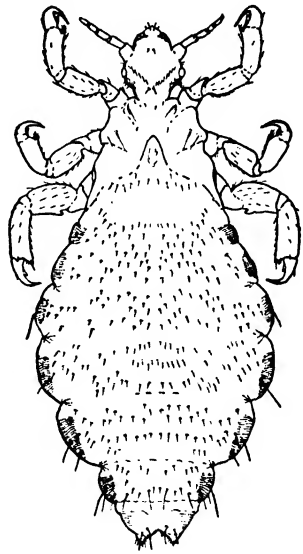

FIG. 233. The cootie or body louse *Pediculus humanus*. (Redrawn from Ferris)

The cootie has vied with the mosquito in shaping the destiny of history. Cooties transmit typhus fever and trench fever, which until recent years have been the scourges of northern armies, especially in winter. Under unsanitary crowded camp or trench conditions, soldiers with heavy clothing provided ideal hosts for cooties. Typhus and trench fever have occurred in outbreak form and with disastrous results throughout many European armies. Napoleon's army in Russia was decimated as much by louse-borne disease as by hunger and exposure. The opposing Russian army suffered fully as much from typhus as the French army. Many claim that the cooties won the campaign, defeating both armies.

In World War II the control of lice by treatment of entire city populations with DDT stopped outbreaks of typhus which had reached epidemic proportions. The miraculous results achieved in Naples in 1944 represent one of the most significant modern advances in the annals of preventive medicine.

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Ferris, G. F., 1934. A summary of the sucking lice (Anoplura), Entomol. News 45:70–74, 85–88.

Riley, W. A., and O. A. Johannsen, 1932. Anoplura, Medical Entomology, pp. 125–142, figs. 59–63. New York, McGraw-Hill Book Co., Inc.

Order HEMIPTERA

Bugs and Their Allies

A large assemblage of diverse insects, characterized chiefly by (1) piercing–sucking mouthparts which form a beak, (2) incomplete

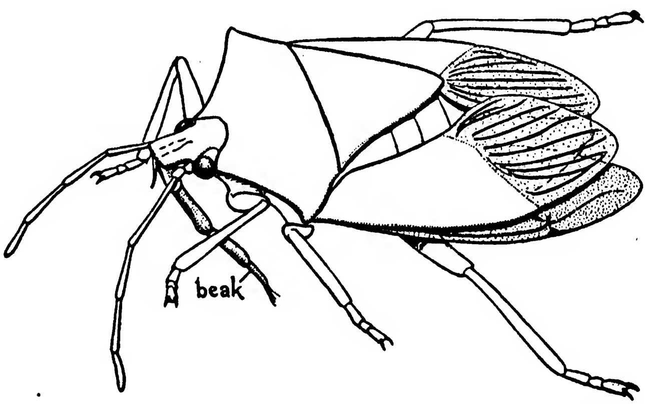

Fig. 234. A typical stink bug, illustrating beak and wings. (From Illinois Natural History Survey)

metamorphosis, and (3) usually the possession of wings, fig. 234. With few exceptions the compound eyes are large, the antennae four- to ten-segmented, the individual segments frequently long, two pairs of wings are present and have relatively simple or reduced venation, and the abdomen has no cerci.

The order derives its name from the structure of the front wing in many families, figs. 234 and 236, in which the basal portion is hard and thick, called the *corium,* and the apex is thinner and transparent, called the *membrane.* The corium approaches in texture the hard wing cover or elytron of beetles, hence the name "hemelytron" is often applied to this half and half type of front wing.

The Hemiptera are divided into two suborders, the Heteroptera and Homoptera. The families represented in North America fall definitely into one suborder or the other, but a few families occurring in other regions appear to present intergrading conditions between the two groups.

Key to Common Families

1. Hind leg without tarsal claws and having both tarsus and pretarsus flattened and bearing a dense fringe of long hair down each side, fig. 235*A;* middle tarsus having normal tarsal claws (part of **Heteroptera**) 2
   Hind tarsus having tarsal claws similar to those on middle tarsus; hind leg usually without a long fringe but occasionally having one, fig. 235*C* 3
2. Beak forming a triangular striated piece that appears as a ventral sclerite of the head, fig. 235*G;* middle tarsus having extremely long claws, fig. 235*B;* front tarsus comblike .... **Corixidae,** p. 284
   Beak cylindrical and rodlike, curving back from the ventral portion of the head, as in fig. 235*L;* front and middle legs usual in shape
   Notonectidae, p. 285
3. Beak arising from front or venter of head, fig. 235*L;* the venter of the head posterior to beak forming a sclerotized bridge or gula (**Heteroptera**) 4
   Beak arising from posterior margin of head, fig. 237*L;* no gula present behind it (**Homoptera**) 28
4. Antennae shorter than head, usually recessed in a concavity beneath the eyes or under the lateral margin of the head, as in fig. 235*G* 5
   Antennae at least as long as the head, usually extending free from it, fig. 242, sometimes fitting into a pronotal groove when at rest 7
5. Ocelli present. Small toadlike bugs, fig. 237*E,* found along the margins of lakes and streams .... **Gelastocoridae**
   Ocelli absent. Forms living in water, sometimes flying and attracted to lights 6
6. Tarsi 1-segmented, front tarsus with only a minute tooth or none, fig. 235*D;* apex of abdomen with a long or short respiratory tube, fig. 238, each blade of which is concave mesally, the two fitting together to make a hollow tube; hind legs slender and without fringes of long hair .... **Nepidae**
   Tarsi 2-segmented, front tarsus with a stout curved tooth, fig. 235*C;* apex of abdomen at most with a pair of short flat respiratory filaments; hind tibia and tarsus often flattened, always with fringes of long hair for swimming
   Belastomatidae, p. 286
7. Head extremely long and slender, slightly bulbous at apex, where beak arises, the eyes situated at the middle of what appears to be a long neck; rest of body also very slender, fig. 239 .... **Hydrometridae**
   Head much stouter, fig. 235*I,* or eyes not situated on the neck, fig. 235*J* 8

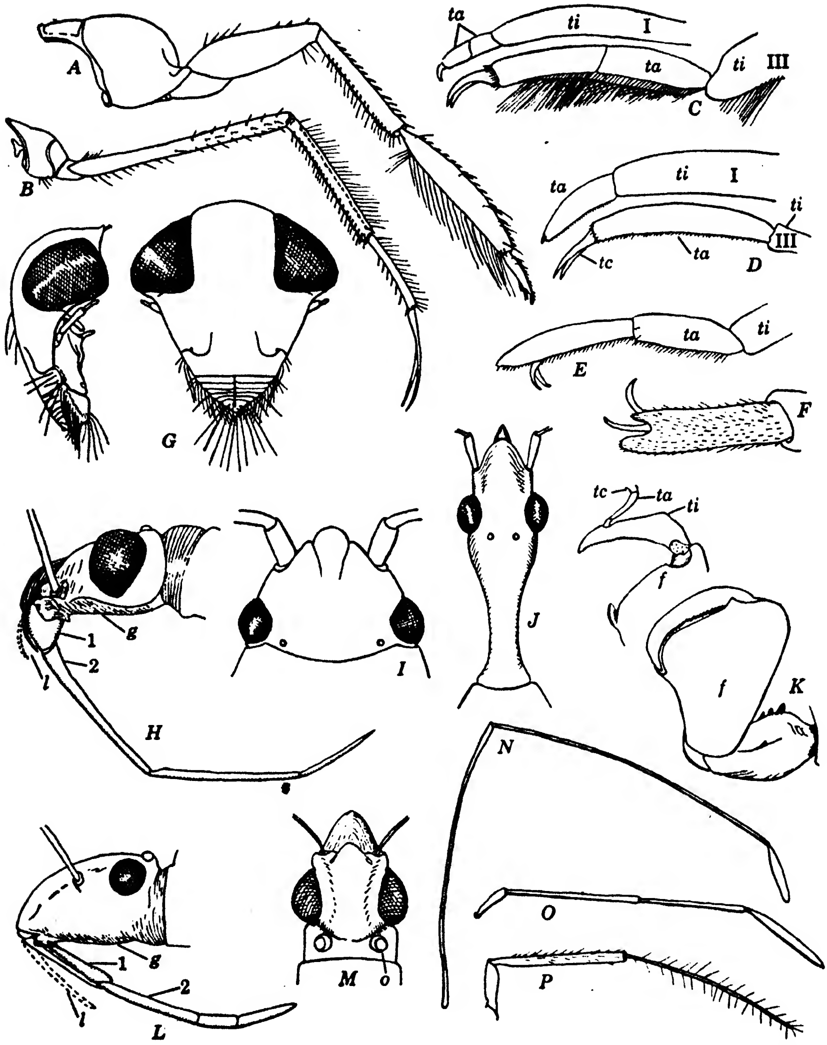

FIG. 235. Diagnostic characters of Hemiptera. *A*, and *B*, hind leg and middle leg of *Corixa*, Corixidae; *C*, front and hind tarsi of *Zaitha*, Belastomatidae; *D*, front and hind tarsi of *Nepa*, Nepidae; *E* and *F*, front tarsus, lateral and dorsal aspect of *Gerris*, Gerridae; *G*, head of *Corixa; H*, head of *Nabis*, Nabidae; *I*, head of *Lygaeus*, Lygaeidae; *J*, head of *Myodocha*, Lygaeidae; *K*, front leg, inset showing structure of tarsus of *Phymata*, Phymatidae; *L*, head of *Alydus*, Coreidae; *M* and *N*, head and antenna of *Jalysus*, Neididae; *O*, antenna of *Myodocha*, Lygaeidae; *P*, antenna of *Lyctocoris*, Anthocoridae. *f*, femur; *g*, gula; *l*, labrum, *o*, ocellus; *ta*, tarsus; *tc*, tarsal claws; *ti*, tibia.

8. Front leg having femur and tibia forming a large grasping device, femur swollen and triangular, tibia curved and closing against the end of femur, fig. 235*K* . . . . **Phymatidae**
Front leg having femur elongate or swollen, fig. 248, but never triangular 9

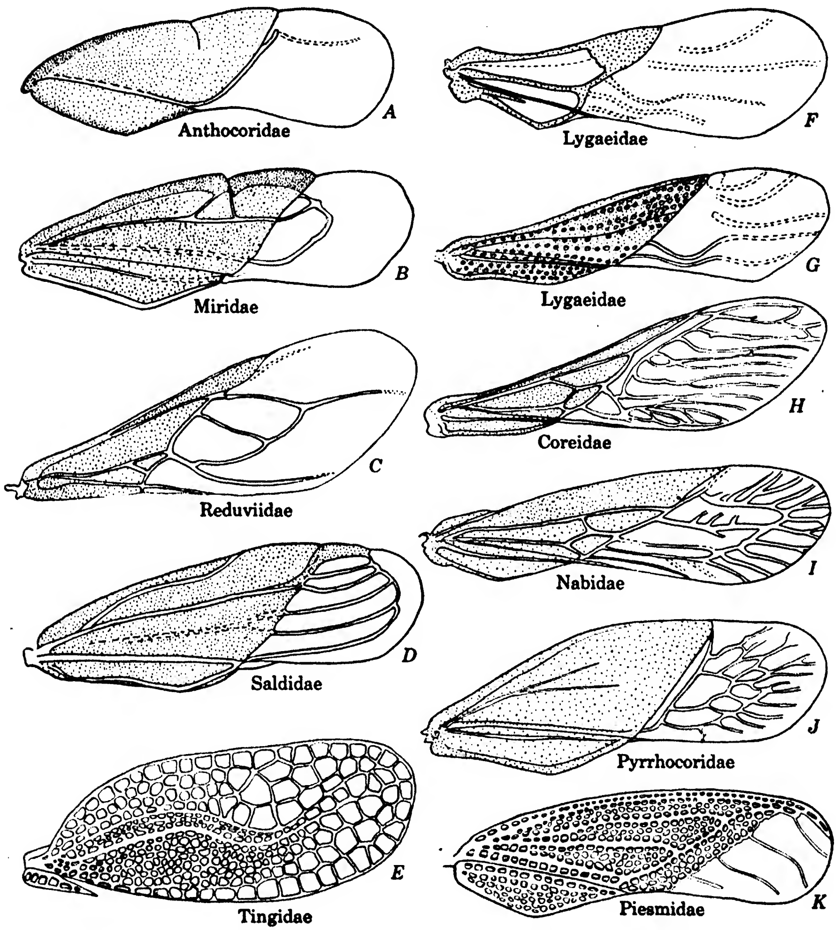

FIG. 236. Elytra or forewings of Hemiptera. *A, Triphleps; B, Lygus; C, Pselliopus; D, Salda; E, Gargupha; F, Blissus; G, Myodocha; H, Alydus; I, Nabis; J, Euryophthalmus; K, Piesma.*

9. Claws of front tarsus inserted before apex, fig. 235*E, F* 10
Claws of front tarsus attached at apex, as in fig. 235*C* 11
10. Middle pair of legs attached far from front legs, close to hind legs; hind femur very long, fig. 242; beak 4-segmented . . . . **Gerridae,** p. 287
Middle pair of legs attached about midway between front and hind legs; hind femur only moderately long; beak 3-segmented . . . . **Veliidae**

11. Scutellum very large, reaching about one-half or more distance from posterior margin of pronotum to end of folded wings, fig. 237*B–D*; antennae usually 5-segmented. **(Pentatomidae, p. 294)** 12
 Scutellum much smaller, reaching about a quarter of the distance from pronotum to tip of body, fig. 237*A*; antennae usually 4-segmented 15
12. Tibia armed with rows of thick thornlike spines, fig. 237*F* 13
 Tibia having series of short even spines, occasionally with a few scattered, very slender hairs, fig. 237*G* 14
13. Scutellum triangular and not very large, as in fig. 237*B* .... **Cydninae**
 Scutellum large and U-shaped, covering most of abdomen, fig. 237*D* **Thyreocorinae**
14. Scutellum U-shaped and very wide, covering almost all of abdomen, the sides of scutellum curved mesad at extreme base, as in fig. 237*D* .... **Scutellerinae**
 Scutellum V-shaped, fig. 237*B*, or, if U-shaped, then never larger than in fig. 237*C*, and slightly contracted just beyond base .... **Pentatominae**
15. Front wing abbreviated, with no membrane, and reaching at most to middle of abdomen, fig. 244 16
 Front wing normal, with a large apical membrane, or reaching well beyond middle of abdomen, fig. 236 17
16. Body flat and wide; front wing short, broad, and scalelike, only barely reaching over base of abdomen; sides of pronotum large, round, and flangelike, fig. 244; beak 3-segmented; antennae long and slender .... **Cimicidae,** p. 287
 Body narrower, or otherwise different from foregoing, having either a 4-segmented beak, different-shaped wing, or short antennae. A few genera, most of them rare, difficult to key to family, belonging to **Anthocoridae, Miridae, Aradidae, Lygaeidae,** or **Nabidae;** and all nymphs of Heteroptera families listed beyond this point. This entire wingless group is not keyed farther here.
17. Hemelytra large, covering entire abdomen and reticulate over their entire surface with a netlike pattern, with little or no distinction between corium and membrane, fig. 236*E* .... **Tingidae,** p. 293
 Hemelytra with a definite apical membrane, fig. 236, all except *E* 18
18. Membrane of hemelytron having one or two large basal cells, and only one or two short spurlike veins extending distally from these, fig. 236*B, C* 19
 Membrane of hemelytron having either no closed cells, fig. 236*A*, or at least five or six veins running through the membrane, fig. 236*D, H, I, J* 20
19. Ocelli prominent, two in number; membrane of hemelytron having a long vein proceeding from top of upper closed cell, fig. 236*C* .... **Reduviidae,** p. 287
 Ocelli absent; membrane with a vein proceeding only from bottom of lower closed cell, or such a vein lacking, fig. 236*B* .... **Miridae,** p. 287
20. Antenna having first two segments stout, last two threadlike, forming a slender terminal filament, fig. 235*P*; ocelli present but small; hemelytral membrane with only one or two weak veins, fig. 236*A* .... **Anthocoridae**
 Antenna having one or both of the two apical segments as thick as the first or second, fig. 235*N, O* 21
21. Hemelytral corium extending markedly beyond a ridgelike oblique vein near apex of corium, fig. 236*K*; corium entirely reticulate .... **Piesmidae**
 Hemelytral corium not extending beyond an apical oblique vein, fig. 236*H–J*, or not having such a vein, fig. 236*G* 22

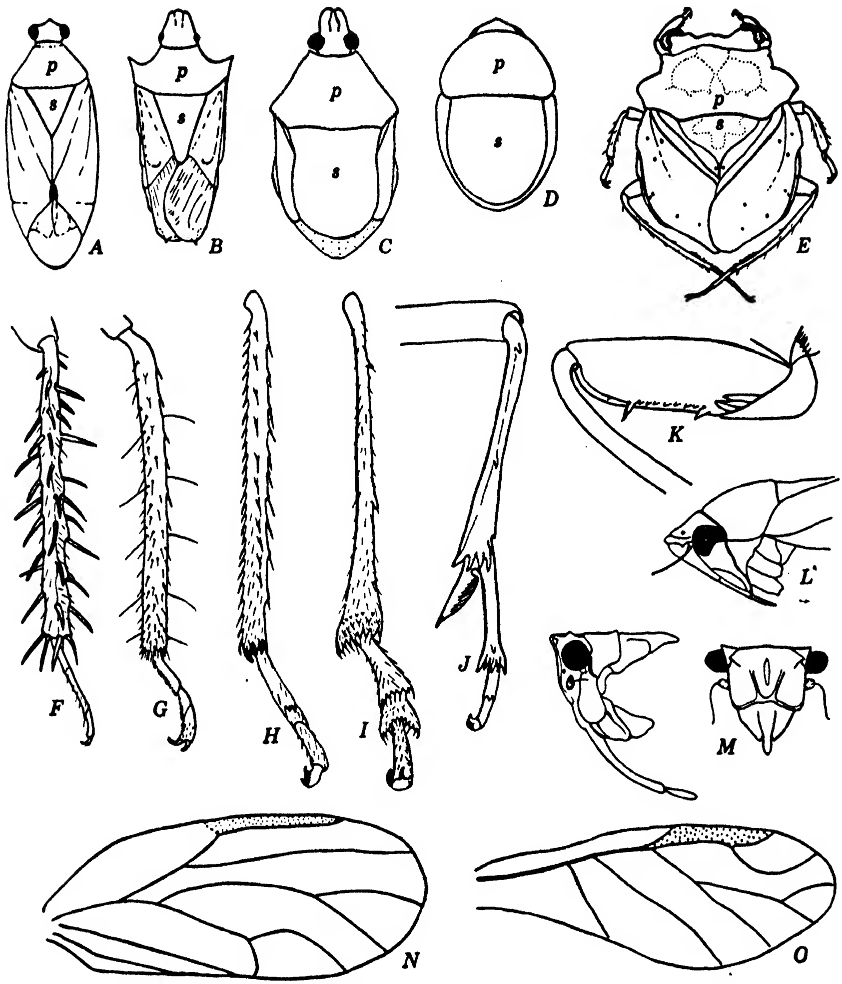

FIG. 237. Diagnostic characters of Hemiptera. *A*, outline of *Lygus*, Miridae; *B*, outline of *Solubia*, Pentatomidae; *C*, outline of *Stiretrus*, Pentatomidae; *D*, outline of *Corimelaena*, Pentatomidae; *E*, *Gelastocoris*, Gelastocoridae; *F*, hind tibia and tarsus of *Pangaeus*, Pentatomidae; *G*, hind tibia and tarsus of *Thyanta*, Pentatomidae; *H*, hind tibia and tarsus of *Aulacizes*, Cicadellidae; *I*, hind tibia and tarsus of *Aphrophora*, Cercopidae; *J*, hind tibia and tarsus of *Stenocranus*, Fulgoridae; *K*, front femur of *Pacarina*, Cicadidae; *L*, head of *Gypona*, Cicadellidae; *M*, head, lateral and anterior views of *Poblicia*, Fulgoridae; *N*, wing of *Psylla*, Psyllidae; *O*, wing of *Aphis*, Aphididae.

22. No ocelli present 23
Two ocelli present 24
23. Flat wide warty bugs, fig. 248; tarsus 2-segmented, the first segment short; hemelytra often small, the periphery of the abdomen extending considerably beyond them .... **Aradidae**, p. 293
Stout insects, the body deep; tarsus 3-segmented, the first segment long; hemelytra larger, fig. 236*J*, covering all abdomen except tip and sides near apex **Pyrrhocoridae**

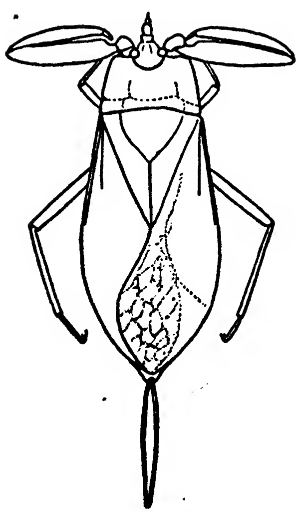

FIG. 238. *Nepa*, Nepidae. (From Hemiptera of Connecticut)

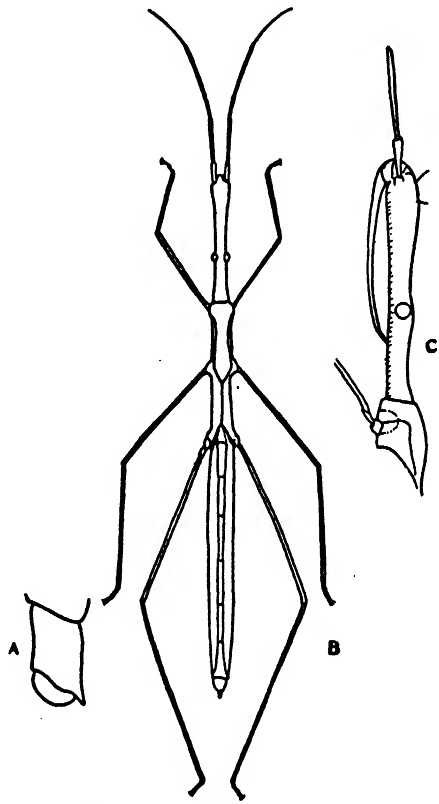

FIG. 239. *Hydrometra*, Hydrometridae. (From Hemiptera of Connecticut)

24. Hemelytral membrane having four or five large and fairly regular closed cells and no other venation, fig. 236*D*; oval fairly flat bugs found on stream and lake shores .... **Saldidae**
Hemelytral membrane having either an irregular network of cells or only one or two small ones, fig. 236*F–I* 25

25. Membrane having a series of about 15 irregular veins, at least on apical portion, fig. 236*H, I*............26
Membrane having only five or six veins across it, fig. 236*F, G*............27
26. First segment of beak short and conelike, thicker than the second, fig. 235*H*; front femur thickened, front tibia armed inside with a double row of short black teeth............**Nabidae**
First segment of beak cylindrical and long, similar in general shape to second segment, fig. 235*L*; front femur usually more slender, front tibia never with inner rows of black teeth............**Coreidae,** p. 292
27. Each ocellus situated behind an eye, at the base of a distinct swelling, fig. 235*M*; extremely slender and elongate bugs, with long and slender legs and antennae; last segment of antenna short and oval, forming a small club, fig. 235*N*............**Neididae**
Ocelli situated closer to or between eyes, and not at the base of a swelling, fig. 235*I, J*; chiefly robust short insects or having short legs; antennae either short, fig. 235*O*, or not clubbed............**Lygaeidae,** p. 291
28. Having wings, which are sometimes reduced to short scales............29
Completely wingless species............37
29. Front femur greatly enlarged in comparison with middle femur, fig. 237*K*; three ocelli present............**Cicadidae,** p. 296
Front femur no larger than middle femur; two or no ocelli present............30
30. Antennae arising from sides of head, situated beneath or behind eyes, fig 237*M* **Fulgoridae,** p. 296
Antennae arising from front of head between eyes, fig. 237*L*............31
31. Pronotum enlarged dorsally into a large structure which covers most of head and body and may be highly ornamented with spines and processes, fig. 252 **Membracidae,** p. 296
Pronotum small, without dorsal enlargement............32
32. Pronotum forming a broad shield which covers the greater part of the mesonotum, fig. 256; tarsus 3-segmented, fig. 237*H–J*............33
Pronotum forming a narrow collar which does not extend back over the mesonotum, fig. 259; tarsus 1- or 2-segmented............34
33. Hind tibia bearing a double row of spines down its entire length, its apex usually not enlarged, fig. 237*H*............**Cicadellidae,** p. 299
Hind tibia with only scattered spines except at apex, which is enlarged and armed with a prominent crown of spines, fig. 237*I*............**Cercopidae,** p. 296
34. Having only one pair of wings............male **Coccoidea,** p. 303
Having two pairs of wings............35
35. Wings milky-opaque, covered with a fine powdery white wax **Aleurodidae,** p. 300
Wings transparent or patterned, not covered with a waxy secretion............36
36. Front wing with R_s very long and *Cu* branched, fig. 237*N*; abdomen never with cornicles............**Psyllidae,** p. 300
Front wing with R_s short and *Cu* unbranched, fig. 237*O*; abdomen in many species having a pair of lateral tubes or cornicles, fig. 259.. **Aphididae,** p. 300
37. Eyes large, antennae situated at sides of head below or behind eyes, fig. 237*M* **Fulgoridae,** p. 296
Either eyes rudimentary or absent, or antennae situated on front of head between eyes, fig. 259............38

38. Tarsus 1-segmented; body covered with a hard shell, waxy secretions, or a detachable scale, fig. 260; abdomen never having cornicles. . **Coccoidea,** p. 303
Tarsus 2-segmented; body at most with waxy secretions; abdomen often having a pair of conspicuous cornicles or tubes, fig. 259. . . . . . . **Aphidoidea,** p. 300

Suborder HETEROPTERA

Bugs

This suborder contains a wide variety of forms ranging from a few millimeters to a few inches in length, and including terrestrial, semi-aquatic and aquatic types. The antennae are four- or five-segmented, and the eyes are well developed except in the ectoparasitic family Polyctenidae.

The nymphs of all forms resemble the adults in general outline, but differ uniformly in having dorsal stink glands on the abdomen. In this respect they differ also from the nymphs of the Homoptera.

The eggs are usually laid singly or in groups glued to stems or leaves. In some forms the eggs are inserted into plant stems or, rarely, into damp sand.

The suborder contains about equally predaceous species and plant-feeding species; often both types occur in the same family. The predaceous species feed chiefly on smaller insects. In certain species of the plant bugs, Miridae, the predaceous habit is only partially developed, and insect blood serves merely to supplement the principal diet of plant juices. The mixture of food habits in the same families has resulted in some queer anomalies. In the stink bug family Pentatomidae the harlequin bug *Murgantia histrionica* is a serious pest of cabbages; a closely related predatory species, *Perillus bioculatus,* is one of the most effective natural enemies of the dreaded Colorado potato beetle.

Short-Horned Bugs

The members of this group have short antennae, usually recessed under the head and not visible from the dorsal aspect. The group gets its name from this characteristic. The families represented in North America are either aquatic or shore-inhabiting. Of the nine families recognized in our fauna, the Corixidae, Notonectidae, and Belastomatidae are the most common.

Corixidae, Water Boatmen. These bugs, fig. 240, are characterized by the short stout rostrum which looks more like the lower sclerite of the head than like a beak, fig. 235*G*. The front legs are short, flattened, or scoop-shaped; the hind legs are long, flattened, and fringed with combs of bristles. Both nymphs and adults are truly aquatic, swimming in the water and incapable of more than clumsy flopping on land. The fringed hind legs are used for swimming; they swim dorsal side up. The adults leave the water for dispersal flights and may be observed in swarms over bodies of water. Sometimes these swarms are attracted to lights. The eggs are attached to solid

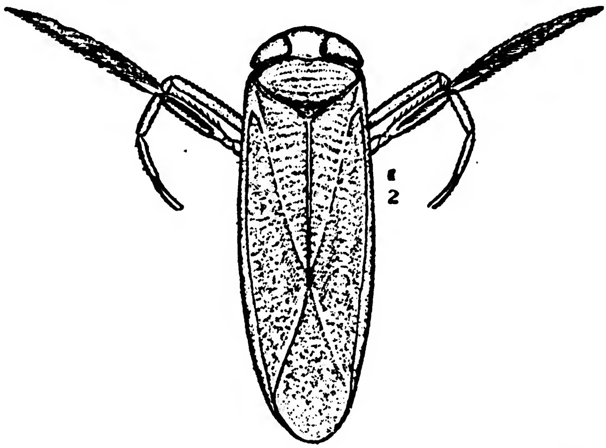

FIG. 240. A water boatman *Arctocorixa alternata.* (From Wellhouse, after Hungerford)

supports such as stones, sticks, and shells in the water. Certain forms, such as *Ramphocorixa,* more often lay their eggs on the body or appendages of the crayfish *Cambarus,* which in some localities may be literally plastered with corixid eggs.

The water boatmen differ from all other Hemiptera in their feeding habits. They feed in the ooze at the bottom of the water, the stylets of the mouthparts darting in and out in unison like a snake's tongue. These stylets draw into the pharynx an assortment of diatoms, algae, and minute animal organisms which constitute their food.

Notonectidae, Backswimmers. In form these aquatic bugs superficially resemble the water boatmen, particularly in the long-fringed oarlike hind legs used for swimming. They are very different, however, in many ways. Most conspicuous is their habit of always swimming on their backs. The coloration of the backswimmers is modified to match this change in swimming position. The ventral side, which is uppermost, is dull brown to match the stream or pond bottom. The dorsal side, which is hidden from above when the insect is swimming, is usually whitish, creamy, or lightly mottled. The beak in the Notonectidae is stout and sharp, used to suck the body contents from small aquatic animals such as Crustacea and small insects on which the backswimmers feed. Many species of backswimmers deposit their eggs on the surface of objects in the water; others insert their eggs into the stems of aquatic plants.

Belastomatidae, Giant Water Bugs. Members of this family are wide and stout, with grasping front legs and crawling and swimming middle

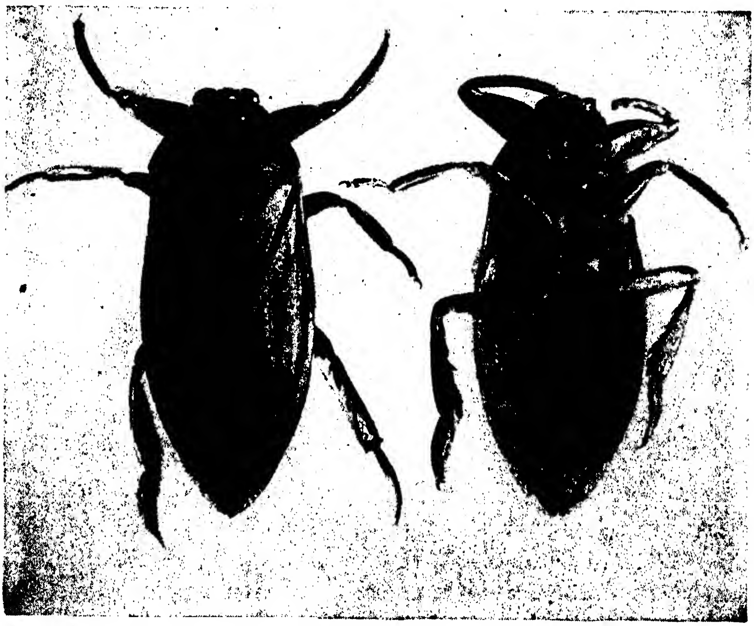

Fig. 241. A giant water bug *Lethocerus americanus*. (From Essig, "College Entomology," by permission of The Macmillan Co.)

and hind legs. They include some of the largest North American Hemiptera, for example, *Lethocerus americanus*, fig. 241, which attains a length of 3 to 4 inches. The giant water bugs have strong beaks. They are predaceous, feeding on insects, snails, small frogs, and small fish. Commonly they are attracted to lights where they draw considerable attention, owing to their ungainly movements and large size.

Long-Horned Bugs

In this group the antennae are exposed and elongate, projecting well in front of the head. Over thirty families are recognized in North America, including a great variety of shapes and habits. The following nine families afford a good cross section of the group.

Gerridae, Water Striders. These are slender bugs with long legs, fig. 242. They live on the surface of water, inhabiting chiefly ponds, the margins of lakes, and the more sluggish backwaters and edges of rivers and streams. The tarsi are fitted with sets of non-wetting hair which allow the bugs to run and stand on the water surface with amazing speed and ease. All species are predators or scavengers, feeding chiefly on other insects that occur on the water surface. They lay their eggs in masses attached to aquatic plants or thrust them into submerged stalks. Several other closely related families live as striders or skaters on the water surface; from these the Gerridae differ in having very long hind femora, which extend considerably beyond the apex of the abdomen.

Reduviidae, Assassin Bugs. These are sluggish predaceous insects, usually medium-sized to large, that wait for living insect prey. Most of our species have fully developed wings, fig. 243, and several have wide foliaceous legs. The nymphs of certain species secrete a sticky substance over the dorsum, on which are carried bits of leaves and debris, providing the animal with very good camouflage. The eggs are laid singly or in clusters, glued to plants or other supports. Assassin bugs sometimes attack man, inflicting a painful burning wound. All the Reduviidae are terrestrial.

Cimicidae, Bedbugs. This family includes only a few species of wide flat insects that feed on the blood of birds and mammals. The fore wings or hemelytra are represented only by short scalelike pads; the hind wings are completely atrophied. They live in bird or mammal nests and in dwellings. Man is attacked by the common bedbug *Cimex lectularius*, fig. 244, which may become an important pest in living quarters of all kinds. During the day the bedbugs hide in cracks and crevices of woodwork, furniture, and debris, emerging at night to seek a blood meal. The female lays up to 200 cylindrical whitish eggs, depositing them in crevices.

Miridae, plant bugs. This family is a very large one, containing about fifteen hundred species, over a third of all known North Ameri-

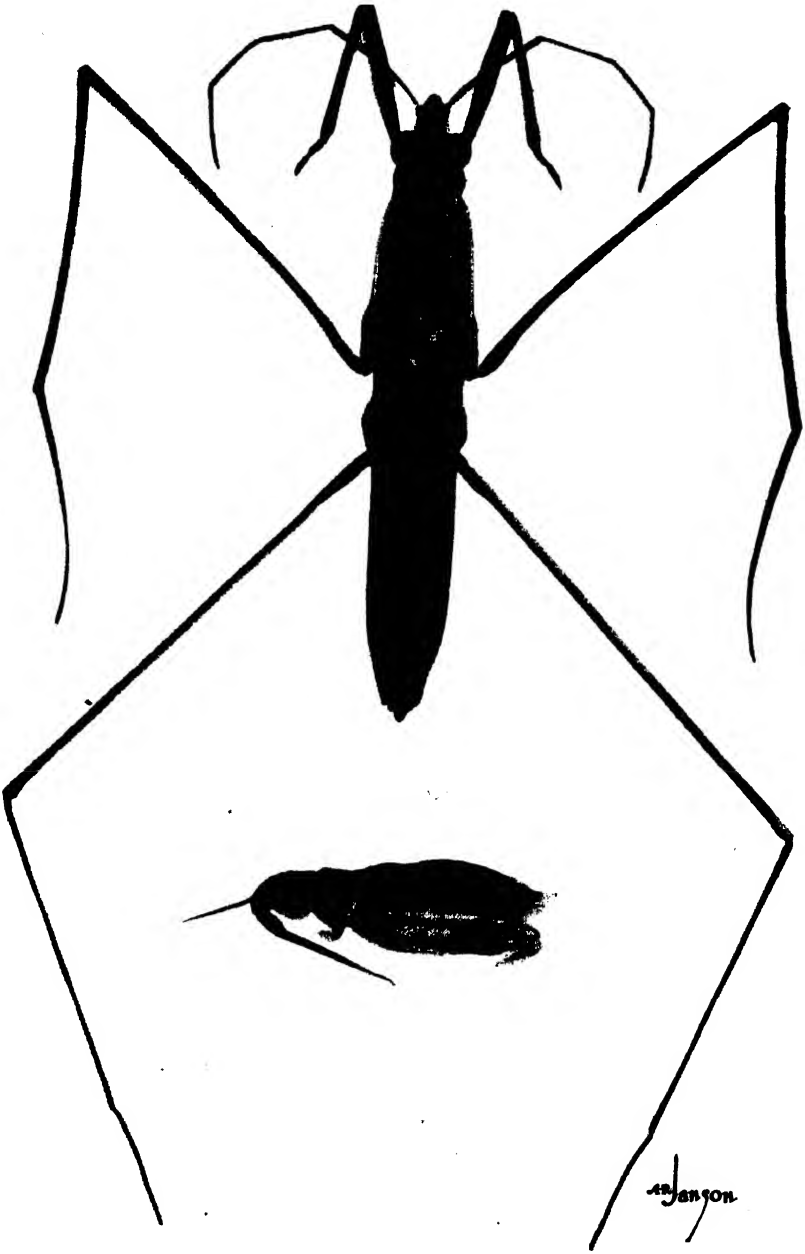

FIG. 242. A water strider, *Gerris dissortis*. (After Drake and Harris)

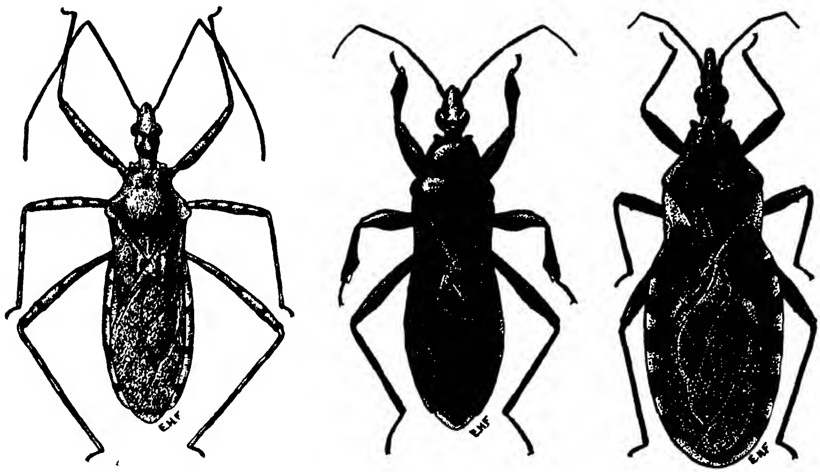

FIG. 243. Three Reduviidae. Left to right, *Pselliopus barberi, Melanolestes picipes,* and *Triatoma sanguisuga.* (Drawings loaned by R. C. Froeschner)

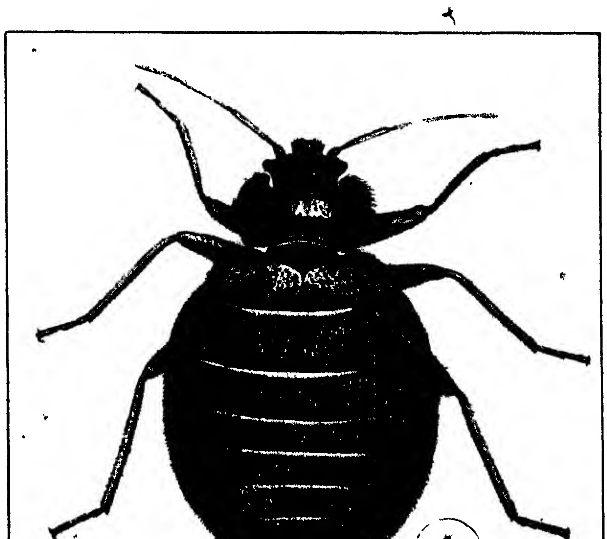

FIG. 244. The common bedbug *Cimex lectularius.* (From Canadian Department of Agriculture)

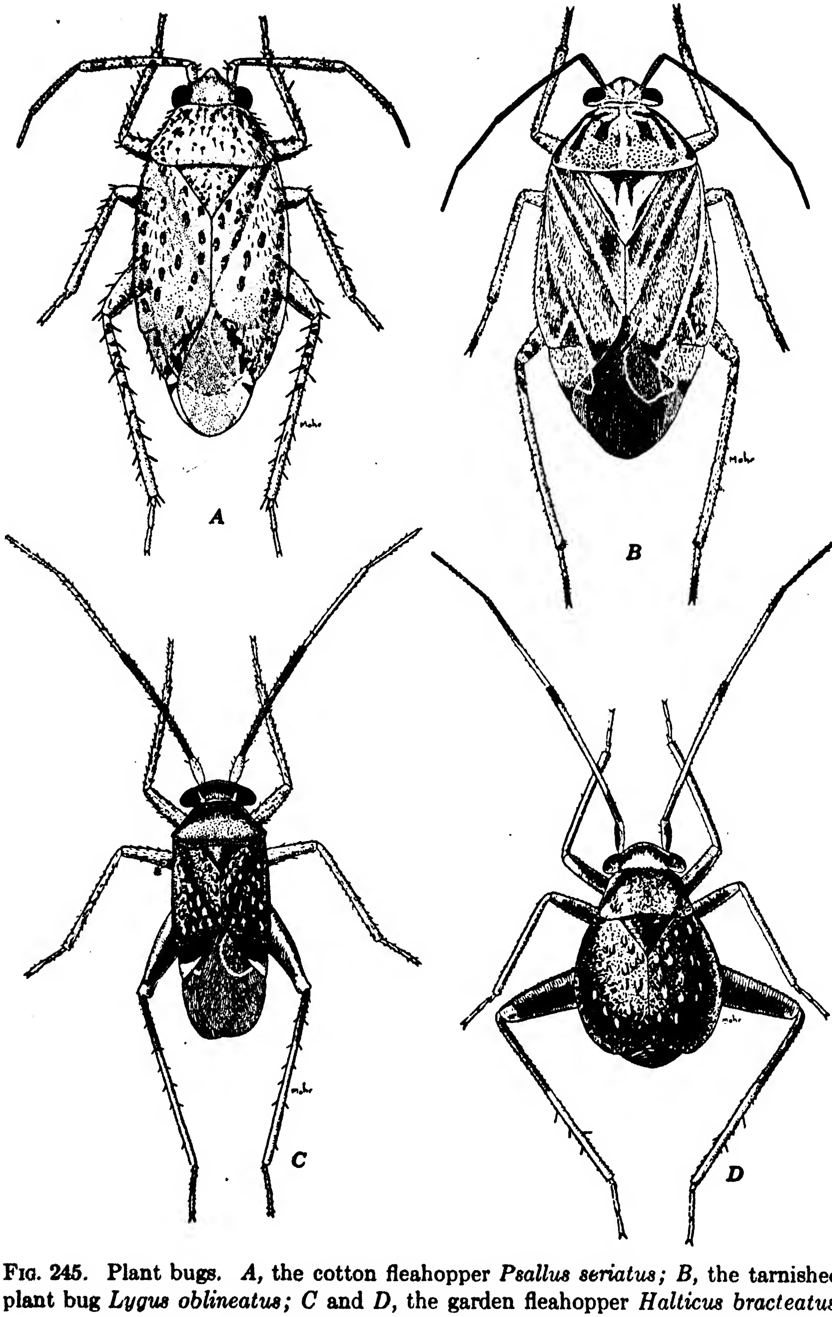

FIG. 245. Plant bugs. *A*, the cotton fleahopper *Psallus seriatus*; *B*, the tarnished plant bug *Lygus oblineatus*; *C* and *D*, the garden fleahopper *Halticus bracteatus*, male and female. (From Illinois Natural History Survey)

can Heteroptera. The plant bugs belong to the series of families having a four-segmented beak and no ocelli. With few exceptions they possess fully developed wings; the hemelytron usually has a distinctive sclerite or *cuneus* in the sclerotized portion and one or two simple cells in the membrane, fig. 236*B*.

Most of the species are plant feeders, many attacking only one or a very limited number of host species. Plant-bug feeding causes etiolation or blossom blight of the host and frequently results in marked commercial loss of certain crops. Some of the more destructive economic species, fig. 245, are the cotton fleahopper *Psallus seriatus;* the garden fleahopper *Halticus bracteatus,* which damages alfalfa, clover, and garden crops such as beans; and the tarnished plant bug *Lygus oblineatus,* a general feeder and a local pest of many crops. Certain genera, including a few striking ant mimics, are predaceous on aphids and other insects.

The plant bug females insert their eggs into dead herbaceous stalks. Most of the species have only a single generation a year, and the winter is passed in the egg stage. A few species, including the tarnished plant bug, hibernate as adults and deposit their eggs the following spring.

Lygaeidae, Chinch Bugs, Lygaeid Bugs. Most North American members of this family are fairly small somber-colored or pale forms. A few genera, such as the milkweed bug *Oncopeltus fasciatus,* fig. 246*A,*

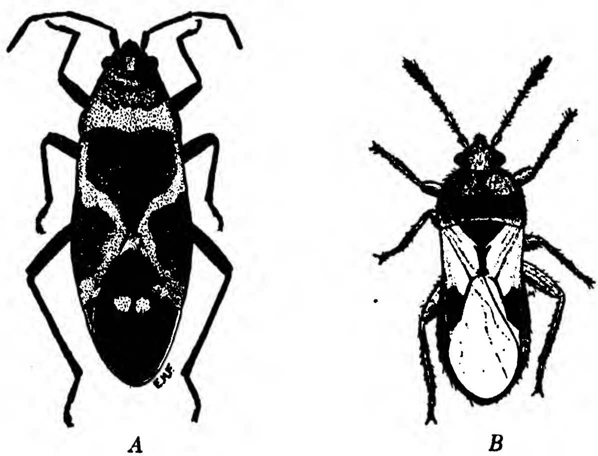

Fig. 246. Lygaeidae. *A,* the milkweed bug *Oncopeltus fasciatus* (drawing loaned by R. C. Froeschner); *B,* the chinch bug *Blissus leucopterus* (from Illinois Natural History Survey).

are strikingly marked with red and black. The diagnostic family characters include the four-segmented beak, lack of ocelli, and a hemelytron with a few irregular veins crossing the membrane, fig. 236*F*. In North America the most important member of this family is the chinch bug *Blissus leucopterus,* fig. 246*B,* which is one of the major insect pests of corn and small grains in the corn-belt states. The chinch bugs hibernate in ground cover as adults. In early spring they feed on grasses and small grains and lay their eggs on the roots and crown of the food plants. The eggs hatch in about 2 weeks, the nymphs feeding on the same plants and maturing in 6 weeks. By the time this brood matures, the original food crop is almost invariably either mature and becoming dry, or it has been overpopulated and offers little in the way of nourishment. When this happens, the entire brood moves out in search of more succulent food. The exodus takes the form of a mass migration, not by flight but by foot. Mature nymphs and newly emerged adults make up the hurrying mass of insects on the march. The search for a better food supply usually ends in a field of corn, now well established and in prime growth. To protect the corn at this time various types of barriers have been developed to trap and kill these marching hordes. The individuals which reach the corn plants establish themselves and produce the second generation. Both the migrating first generation and the second generation feeding to maturity do extensive damage to the corn crop. When mature, the second generation goes into hibernation until the following spring.

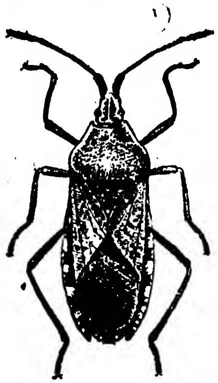

FIG. 247. The squash bug *Anasa tristis.* (After U.S.D.A., B.E.P.Q.)

Coreidae, Squash Bugs, Coreid Bugs. In general characters the Coreidae are like the Lygaeidae, differing chiefly in having many veins in the hemelytron membrane and in having ocelli. Many of these bugs resemble the lygaeid bugs in general shape. Others, such as *Acanthocephala,* bear a striking resemblance to the Reduviidae. Among the coreid bugs are both predaceous and plant-feeding groups. Of the latter the most widely known is the squash bug *Anasa tristis,* fig. 247, which attacks squash, cucumbers, and other cucurbit crops. Its eggs are laid in patches on the leaves and stem of its hosts. There are several generations each year, and winter is passed in the adult stage.

Aradidae, Flat Bugs. This family includes a group of moderate-sized species which are the flattest members of the Heteroptera. They live under the bark of dead trees and are thought to fed on fungi. The tarsi are two-segmented, the antennae and beak four-segmented, and ocelli are lacking. The wings are greatly reduced in size and when folded occupy only a small area of the dorsum, fig. 248. This illustration depicts two common species in eastern and central North America.

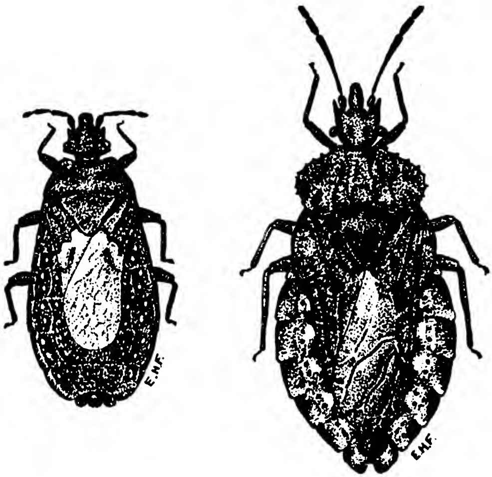

FIG. 248. Flat bugs. *A, Neuroctenus simplex,* and *B, Aradus acutus.* (Drawings loaned by R. C. Froeschner)

Tingidae, Lace Bugs. These are small delicate plant-feeding insects, usually occurring in large colonies. The pronotum and hemelytron are wide, reticulate, and lacelike, extending well beyond the sides of the body; in certain genera the pronotum has a large bulbous mesal lobe which extends forward above the head, fig. 249. The antennae and beak are four-segmented, ocelli are lacking, and the tarsi are two-segmented. The nymphs differ considerably from the adults in general appearance; some are comparatively smooth and scalelike; others are armed with large numbers of long spines. The eggs are laid in or on the leaves of the host plant. The Tingidae are represented in North America by over two hundred species, most of them specific to a single host genus or species. A colony of lace bugs produces a characteristic white-spotted appearance of the leaves that readily betrays the presence of the colony. Examination of alder, oaks, sycamores, hawthorns, apples, birches, and other trees will net many species of lace bugs. Shrubs and herbs also support a considerable fauna.

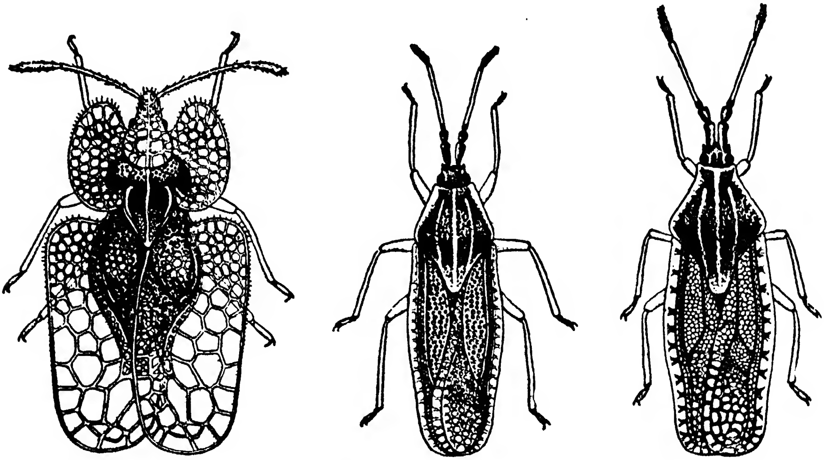

Fig. 249. Lace bugs. Left to right, *Corythuca floridanus, Atheas exiguus*, and *A. insignis*. (After Heidemann)

Pentatomidae, Stink Bugs, Figs. 250, 251. To this family belong many large or medium-sized bugs, most of them broad, many of them mottled with shades of green, gray, or brown. A few are brightly

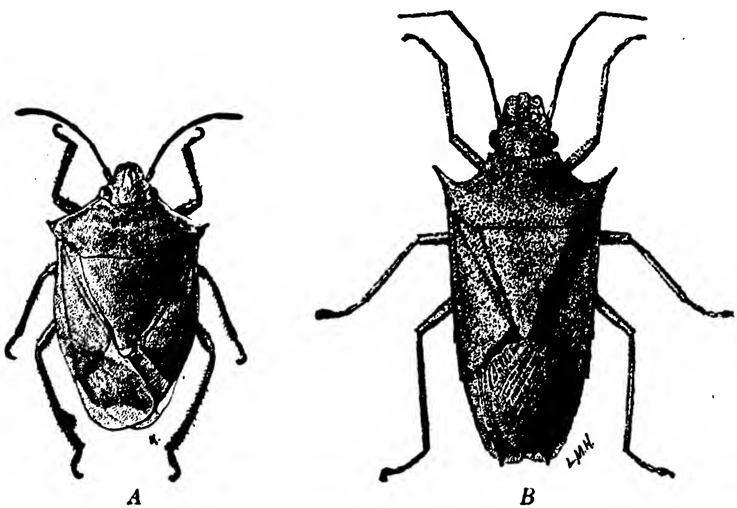

Fig. 250. ***A, Thyanta perditor,*** **and** ***B, Solubea pugnax,*** **two common Pentatomidae. (From Illinois Natural History Survey)**

patterned. A large proportion of the species are predaceous, feeding on a wide variety of other insects. Others are entirely phytophagous, of which the harlequin bug *Murgantia histrionica,* fig. 251, is a familiar example. This bug feeds on cruciferous plants and often does serious damage to cabbage. Three subfamilies, the Scutellerinae,

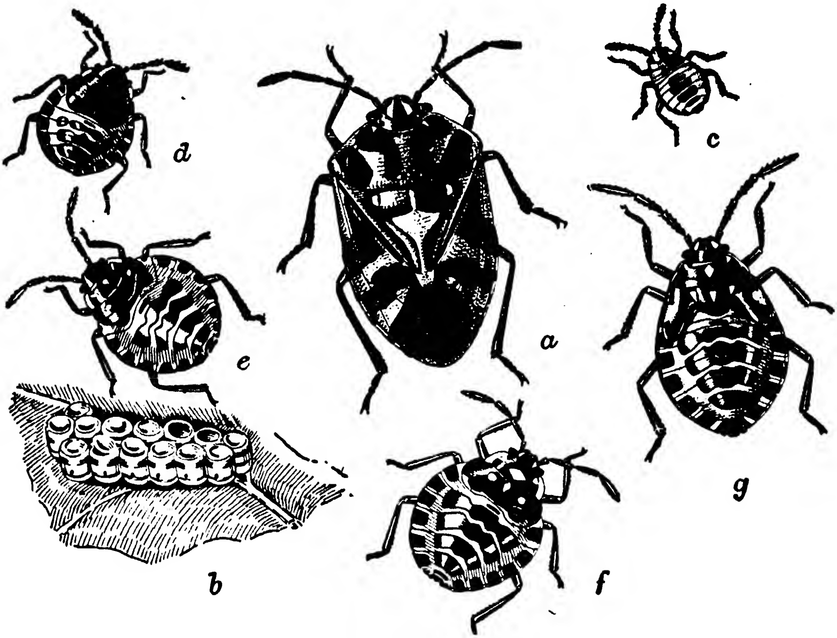

FIG. 251. The harlequin bug, *Murgantia histrionica. a,* adult; *b,* egg mass; *c,* first stage of nymph; *d,* second stage; *e,* third stage; *f,* fourth stage; *g,* fifth stage. (From U.S.D.A., B.E.P.Q.)

Cydninae, and Thyreocorinae, are classed as separate families in some works. The identifying characteristics of these subfamilies, given in the key to families, hold fairly well for the nearctic fauna but break down when considered for the world fauna as a whole.

Suborder HOMOPTERA

Cicadas, Leafhoppers, Aphids, Scale Insects, etc.

This suborder contains two distinct groups of insects: the needle-horned series, containing the cicadas, leafhoppers, and their allies; and the thread-horned series, to which belong the aphids, scale insects, and their allies.

The Needle-Horned Series

These have antennae that are sometimes large at the base, but the apical portion is always in the shape of a slender bristle or needle, fig. 237*L*. The series is further characterized by having the tarsi almost invariably three-segmented, front-wing venation which is relatively complete, and the beak appearing to be a definite part of the head. The insects belonging to this group are all plant feeders. With few exceptions the females have a sawlike ovipositor, by means of which punctures for egg reception are cut in plant stems. The North American fauna of the needle-horned series is composed of about a dozen families. Among them are found many forms of bizarre appearance. Some of the Membracidae, or treehoppers, fig. 252, have the pronotum greatly enlarged and ornamented with ridges, horns, or prongs. The Fulgoridae are a large family, and many resemble leafhoppers, fig. 253. Some of the fulgorids have large foliaceous wings, and others, such as our native *Scolops* and the South American lantern fly, or peanut bug, *Lanternaria phosphorea*, fig. 254 have bizarre projections of the head. Another oddity is the spittle bug family, Cercopidae. The nymphs of this family produce masses of white froth or spittle-like substance and live hidden beneath it. Two well-known and abundant families of the group are the Cicadidae (cicadas) and the Cicadellidae (leafhoppers).

Cicadidae, Cicadas. These are large insects, many North American species measuring 2 inches or more. They are distinguished structurally from related families by having three distinct ocelli on the dorsum of the head. The males have highly developed musical organs, and during warm days and summer evenings they make a shrill noise. The nymphs have enlarged front legs, presumably for digging, and are subterranean, feeding on sap from the roots of deciduous trees.

The nymphal period is long, 2 to 5 years for most species The periodic cicada *Magicicada septendecim*, fig. 255, also called the 17-year locust, has a nymphal life of 13 years in the southern states and 17 years in the northern states. This insect has attracted widespread attention because of the periodic nature of its cycles. In some areas only a single brood occurs, and there the adults appear only every 13 or 17 years. On these occasions they usually appear in huge swarms, and the ovipositing females may cause serious damage to the twigs and branches of fruit and hardwood trees.

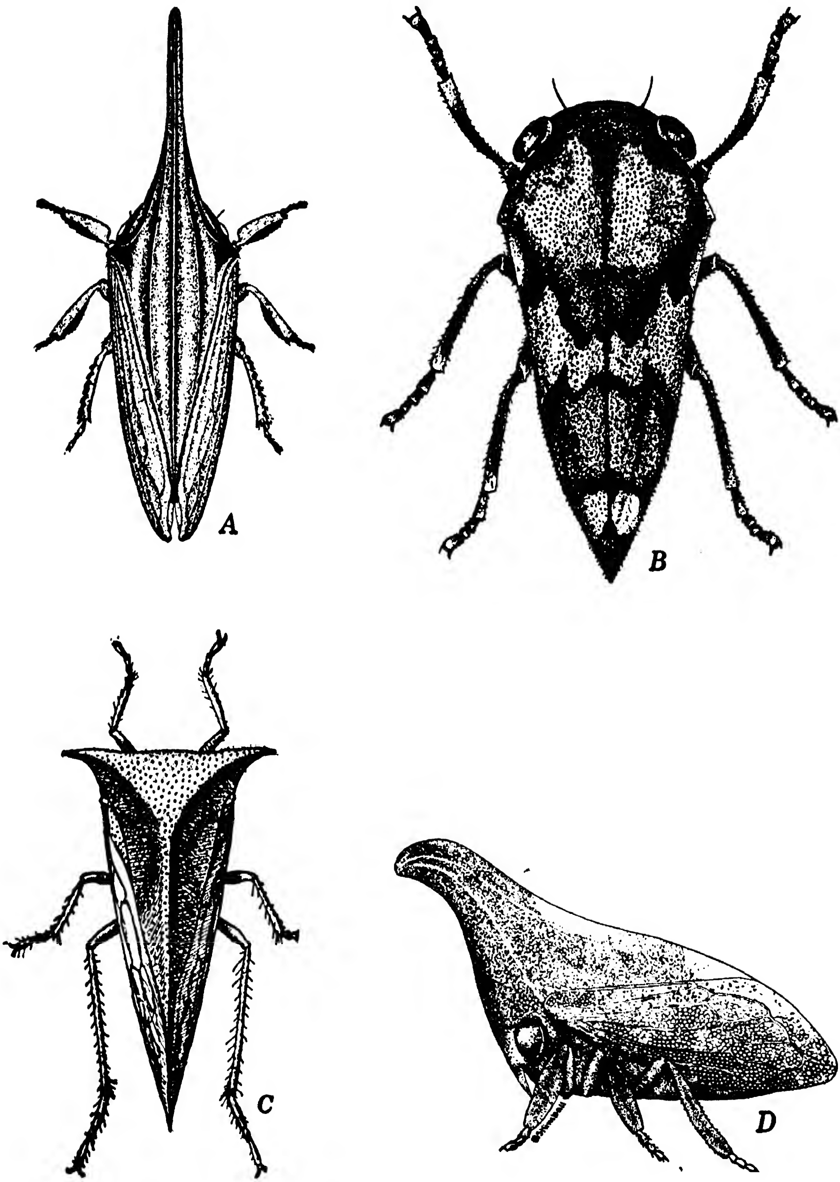

FIG. 252. Treehoppers, Membracidae. *A, Campylenchia latipes; B, Vanduzea triguttata; C, Ceresa bubalis; D, Enchenopa binotata.* (*A, B,* and *D,* courtesy of Kansas State College; *C* after U.S.D.A., B.E.P.Q.)

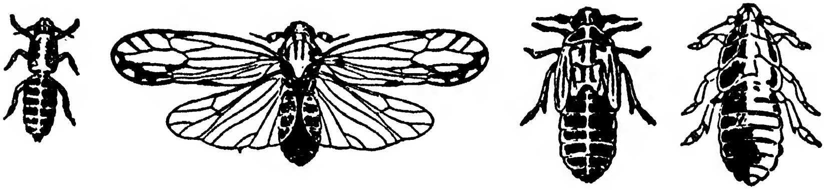

FIG. 253. A fulgorid *Peregrinus maidis.* (After Thomas)

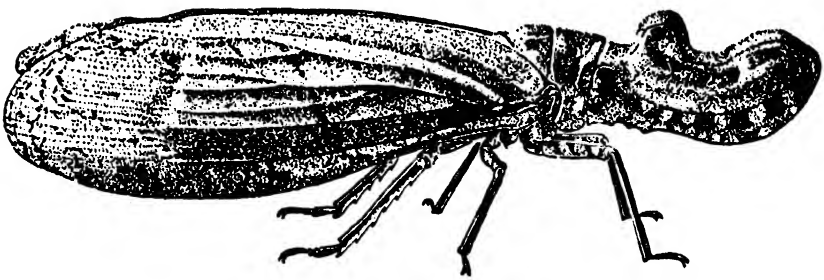

FIG. 254. The peanut bug *Lanternaria phosphorea.* (From Essig, "College Entomology," by permission of The Macmillan Co.)

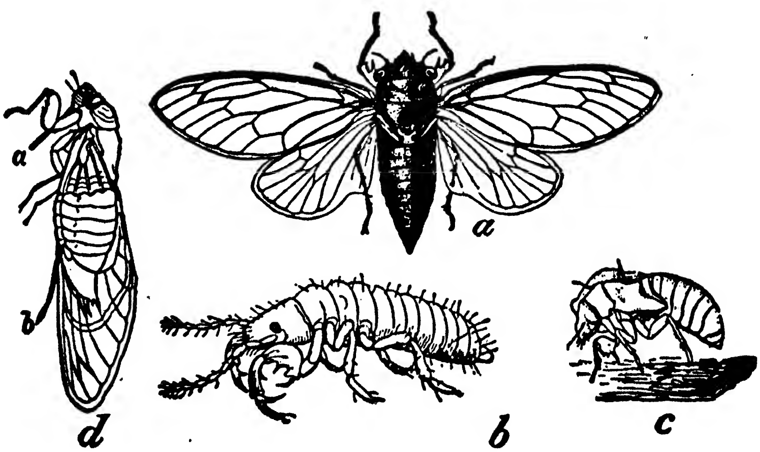

FIG. 255. The periodical cicada *Magicicada septendecim.* *a* and *d,* adults; *b,* nymph; *c,* shed nymphal skin. (From U.S.D.A., B.E.P.Q.)

Cicadellidae, Leafhoppers. This family is the largest in the entire order Hemiptera, represented in North America by over twenty-five hundred species. Leafhoppers are not only numerous in species but also extremely abundant in numbers of individuals. They are probably collected in general sweeping more commonly than any other insect group. Most of these are less than 10 mm. long and have long hind tibiae bearing longitudinal rows of spines, but with neither large spurs nor a crown of spines at the tip. Although a few species are

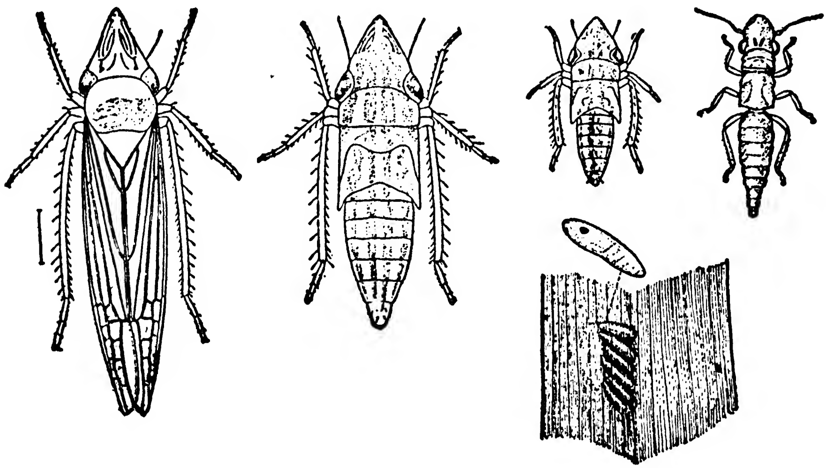

FIG. 256. A leafhopper *Draeculacephala mollipes,* adult, nymphs, and eggs. (From U.S.D.A., B.E.P.Q.)

broad or angular, most are slender and nearly parallel-sided, fig. 256. Female leafhoppers have strong ovipositors which they use to cut slits for eggs in dry plant stalks (usually herbs). Leafhoppers are extremely destructive to certain crops, not only by direct damage caused by feeding, but also because they transmit many plant diseases. The beet leafhopper *Eutettix tenellus* transmits the virus which causes curly top of beets, a most destructive disease to the sugar-beet crop; and *Macropsis trimaculatus* transmits another destructive virus which causes peach yellows.

The Thread-Horned Series

In this series the antennae are either short and stout or long and threadlike, fig. 259, in at least some stage of the life cycle. The wing venation is greatly reduced, and the tarsi have only one or two segments. Various families exhibit extremely interesting phenomena, such as alternation of sexual and parthenogenetic generations and alternation of hosts, as in the aphids, and unique examples of sexual dimorphism and specialization by reduction of locomotor parts, as shown by the scale insects. Because of the occurrence of diverse body forms within the life cycle of a single species, it is difficult to characterize the families with a brief description.

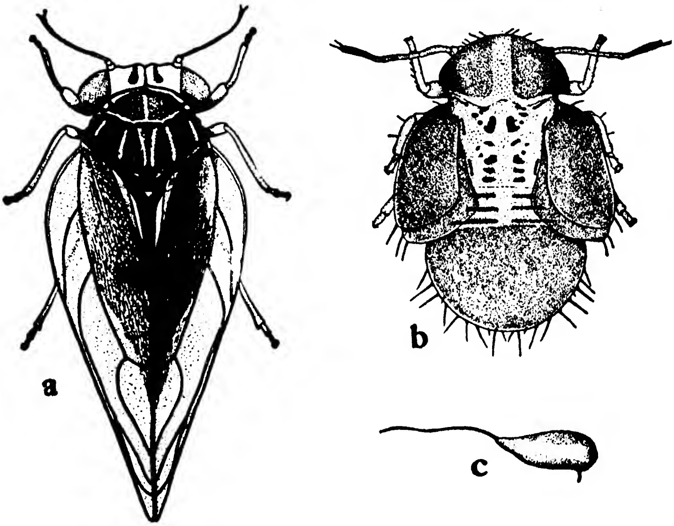

Fig. 257. The pear psylla *Psylla pyricola.* *a,* adult; *b,* nymph; *c,* egg. (From Connecticut Agricultural Experiment Station)

Two families, the jumping plant lice or Psyllidae, fig. 257, and the whiteflies or Aleurodidae, fig. 258, have a simple life cycle in which adults of both sexes are winged and similar in general appearance. In many Psyllidae and all Aleurodidae the later nymphal instars are flat, inactive or sluggish, and scalelike in appearance. The members of both families are small.

All the other families of the thread-horned series are segregated into two large groups: (1) the aphids and their allies, the superfamily Aphidoidea, and (2) the mealybugs and scale insects, the superfamily Coccoidea. Each group contains several families differentiated chiefly by biological characteristics and including many species of great economic importance.

The Aphidoidea, fig. 259, are characterized by (1) the presence of several veins and a stigmal area in the fore wings of the winged forms;

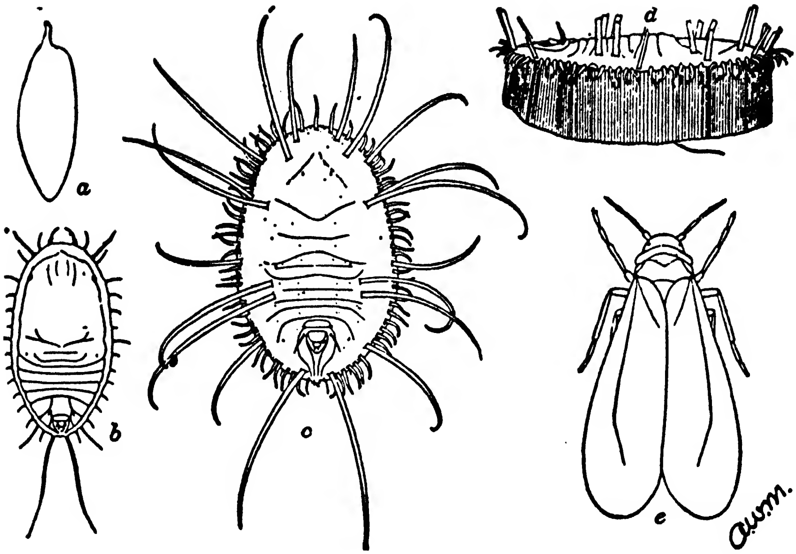

FIG. 258. A whitefly *Trialeurodes vaporariorum*. *a*, egg; *b*, larva, first instar; *c*, puparium, dorsal view; *d*, puparium, lateral view; *e*, adult. (After Morrill)

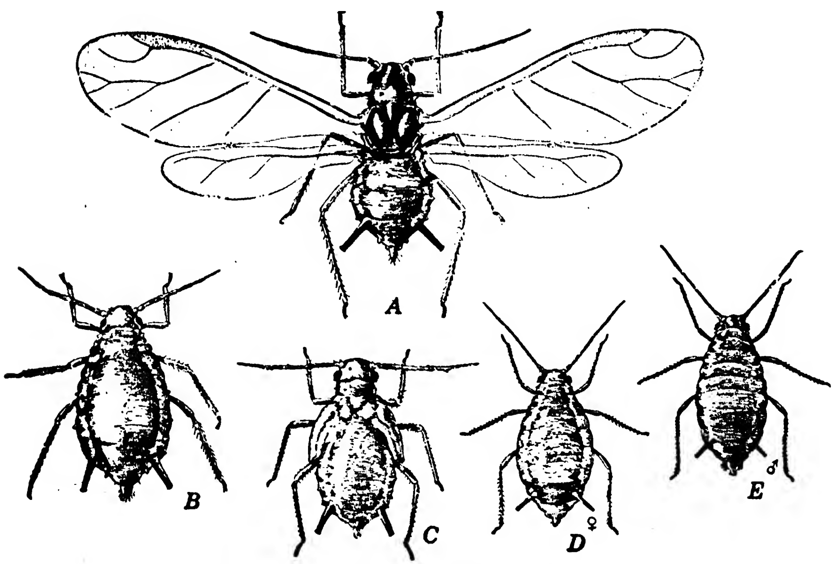

FIG. 259. The green apple aphid *Aphis pomi*. *A*, alate viviparous female; *B*, apterous viviparous female; *C*, nymph of alate; *D*, oviparous female; *E*, male. (From U.S.D.A., B.E.P.Q.)

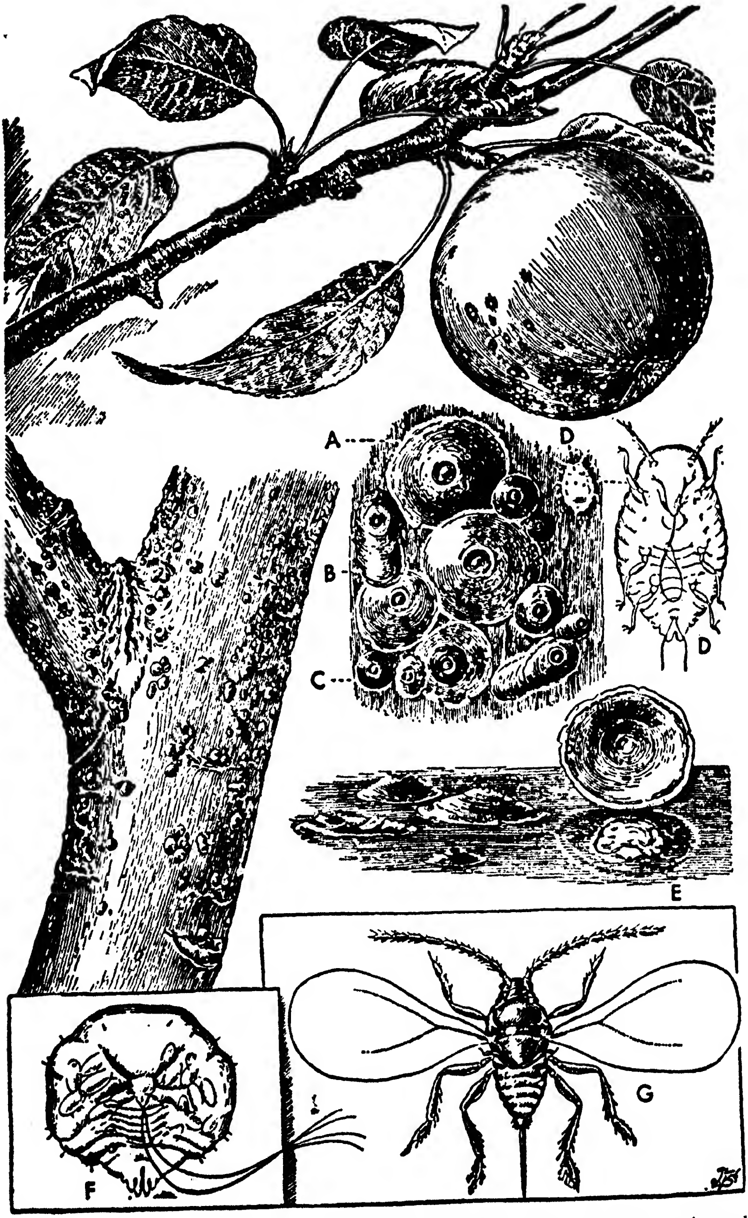

Fig. 260. The San Jose scale *Aspidiotus perniciosus*, infesting apple. *A*, scale of adult female; *B*, scale of male; *C*, first instar young; *D*, same more enlarged; *E*, scale lifted to expose the female body beneath; *F*, body of the female; *G*, adult male. (From U.S.D.A., B.E.P.Q.)

(2) the existence of two-segmented tarsi in most species; and (3) the existence of a complex system of alternating generations including wingless, winged, parthenogenetic, and sexual forms in the life cycle of a single species. This phase is discussed more fully in Chapter 6. The Aphididae, or plant lice, is the most important family in the group. Many species of great economic concern are members of this family, for example, the melon aphid *Aphis gossypii*, a pest of cucur-

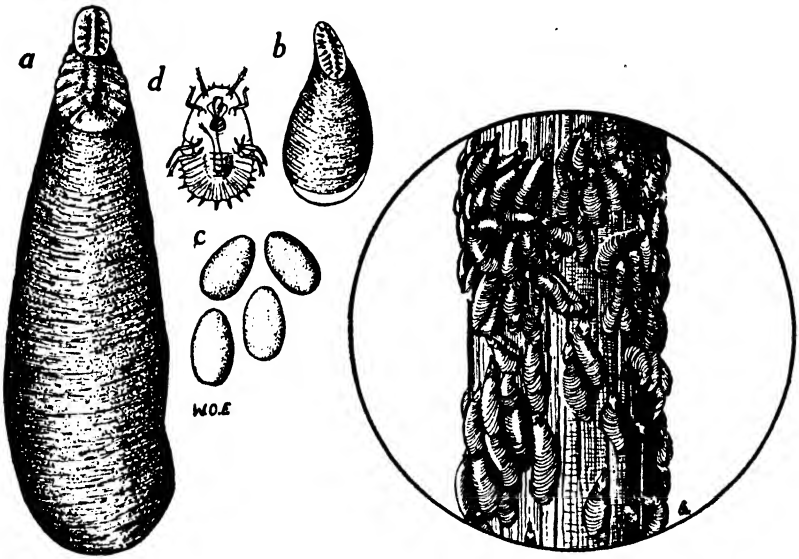

FIG. 261. Oystershell scale *Lepidosaphes ulmi*. *a*, female scale; *b*, male scale; *c*, eggs; *d*, first-instar nymph. (After Blackman and Ellis) In circle, a cluster of scales on lilac stem. (After U.S.D.A., B.E.P.Q.)

bits and cotton; and the green peach aphid *Myzus persicae*, a pest of many crops and the disseminator of many plant diseases.

The Coccoidea, fig. 260, differ in several important respects from the aphids: (1) The females are always wingless, extremely sluggish or completely fixed in position, and are covered by a waxy secretion or a tough scale, or have a hard integument, as in the family Coccidae; (2) the males are small and delicate and have a single pair of wings with only one or two simple veins; and (3) the life cycle is relatively simple.

The family Diaspididae, fig. 260, is one of the most important in the scale insect group. The females are the sedentary, small, scalelike or cushion-like insects found on many species of trees. The actual insect is a delicate oval body hidden beneath the scale, which is a protective covering. The appendages are extremely reduced, the body becoming little more than an egg sac at maturity. As the eggs are gradually discharged, the body shrinks, so that the entire egg mass is laid within the protective covering of the scale. The first-instar nymphs are minute and extremely active. They crawl with rapidity in all directions and thus effect the widespread distribution of these scale insect species. After the first molt, the nymphs become sedentary, and each forms a scale. Several species of the family are among the most destructive insects known to commercial agriculture. The San Jose scale *Aspidiotus perniciosus,* fig. 260, is a persistent pest of deciduous fruit trees and many ornamentals; before advent of oil sprays it threatened to wipe out several of the fruit crops in many areas in the United States. The cosmopolitan oystershell scale *Lepidosaphes ulmi,* fig. 261, is a common pest of almost all deciduous trees and shrubs in the United States.

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Series Holometabola

Ten orders are here recognized among present-day members of the Holometabola, all represented in North America. The Holometabola are characterized by the specialization of the immature instars into larvae and pupae. In some instances these stages present more well-defined differences between the orders than do the adults.

The most primitive orders of the Holometabola are the "neuropteroid" orders, including the Neuroptera, Megaloptera, Rhaphidiodea, and Mecoptera. In this group of orders, the wings have a large number of both principal veins (frequently much branched toward their tip) and crossveins. In these characters, the neuropteroid groups resemble the primitive orthopteroid groups and many of the ancient Palaeoptera.

Within the Holometabola, phylogenetic relationships place the order Hymenoptera close to the neuropteroid orders. The generalized, or least specialized, families of Hymenoptera show striking affinities with the Megaloptera and Mecoptera. In the Hymenoptera, however, the principal veins of the wings have coalesced to a remarkable extent, although evidence remains to indicate that the crossveins follow essentially the same pattern as in the Megaloptera.

The remaining orders of the Holometabola may be segregated into two groups: (1) the Coleoptera, in which the front wings, called elytra, are without venation and do not serve as flight organs; and (2) the Trichoptera, Lepidoptera, Diptera, and Siphonaptera, in which the front wings, when developed, are veined and function as normal flying organs. In this latter group the typical venation shows little reduction in the principal veins but has at most eight or nine crossveins, fig. 91.

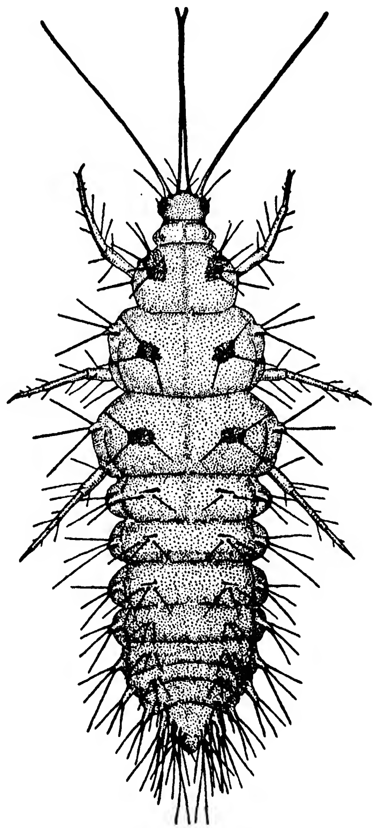


Fig. 262. Larva of a spongefly *Sisyra* sp. (After Townsend)

Order NEUROPTERA

Lacewings, Mantispids

The adults are minute to large insects, usually with two pairs of clear wings having many veins and crossveins, with chewing-type mouthparts, long and multisegmented antennae, and large eyes, fig. 264. The larvae are varied: Most of them are terrestrial and predaceous; one family (Sisyridae) is aquatic, and the larvae feed in fresh-water sponges. All the larvae have thoracic legs, but no abdominal ones, well-developed heads, and mandibulate mouthparts.

The order is represented in North America by ten families, which constitute three very different groups, based on feeding habits of the larvae: (1) sponge feeders (spongeflies), (2) active predators (antlions and their relatives), and (3) sedentary predators (mantispids).

Sponge Feeders. The spongeflies are a small family comprising the Sisyridae. The adults look like typical lacewings, but the larvae are

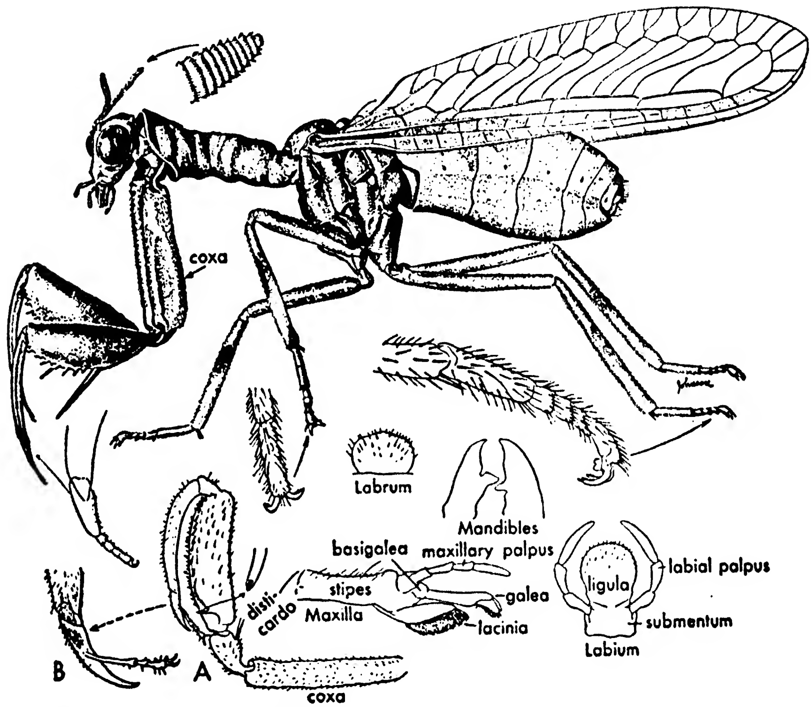
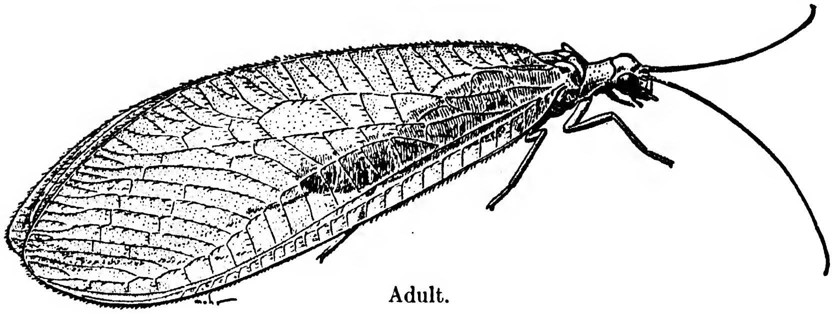


FIG. 263. A mantispid *Mantispa brunnea*. (From Essig, "College Entomology," by permission of The Macmillan Co.)

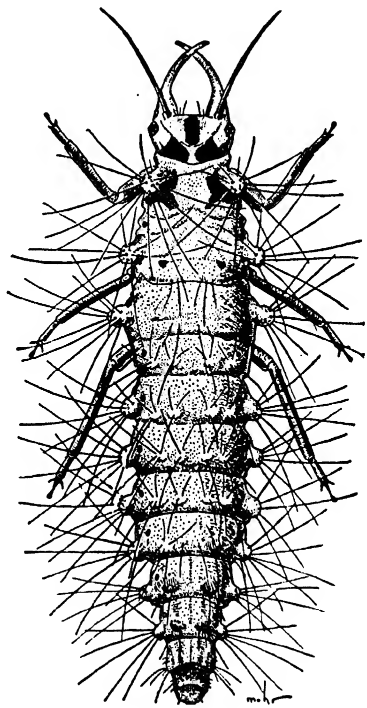
robust creatures that live in and eat fresh-water sponges. Their mouthparts form a long beak which sticks out in front of the larva, fig. 262. Only a few species are known to occur in the nearctic region.

Sedentary Predators. The mantispids, fig. 263, are another small family, Mantispidae. The adults have a striking resemblance to praying mantids. The front legs are greatly enlarged and fitted for grasping insect prey and are attached at the anterior end of the very long pronotum. The larvae feed on egg sacs of spiders or contents of wasp nests. The first-instar larvae are slender and active, and hunt



Adult.

Fig. 264. A lacewing *Chrysopa* sp., adult and larva. (From Illinois Natural History Survey)



Larva.

for a suitable food reservoir. Once this is found, the larvae enter a parasitoid stage, and succeeding instars are grublike and have degenerate legs.

Active Predators. The antlion and aphidlion group embraces most of the order. The adults are delicate, fig. 264, with no striking features other than the transparent abundantly veined wings, which give them the name "lacewings." Most of these insects are relatively slow on the wing. The eggs are laid either attached directly to foliage or at the end of a long hairlike stalk, which is attached to a leaf, fig. 159N. This latter method is used only by the Chrysopidae. The larvae are active, but sluggish and soft-bodied, and frequently bear warts, tubercles, and long hair. The mouthparts are modified for sucking body juices from the prey. The mandibles and ends of the maxillae are long, bladelike, and sickle-shaped, and a maxillary blade fits beneath each mandible; each of these opposing pieces has a groove, the two fitting together to form a canal from near the tip of the mandible into the mouth opening The two mandibular-maxillary blades are thrust into the body of the prey from opposite sides, and its body juices are sucked out through the canals.

The larvae of Chrysopidae, fig. 264, and Hemerobiidae crawl freely about on plants and feed on aphids, other small insects, and insect eggs. Their frequent attacks on aphids have earned them the name "aphidlions." When full grown, the larvae spin a woolly ovoid cocoon under a leaf or in some sheltered spot, and pupation ensues. The larvae of Myrmeleontidae live in sandy soil and dig cone-shaped pits that trap ants and other prey which fall into them. These larvae, called "antlions," differ from the aphidlions only in being more robust. The antlion digs the pit by throwing out sand from the center by upward jerks of the head, using the long mandibles as shovels. The pitfalls may be an inch deep, with sides sloping as much as the texture of the loose sand will allow. The antlion stays in the soil with its head just below the bottom of the crater, constantly in wait for unwary prey. These curious larvae are known to most people by the name "doodlebug." When mature, the larva forms a cocoon in the soil and pupates in it.

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Order MEGALOPTERA

Dobsonflies and Alderflies

Large insects having complete metamorphosis, aquatic larvae, and terrestrial pupae. The adults, fig. 265, have long antennae, chewing-type mouthparts, large eyes, and two pairs of wings. The wings are similar in texture and venation and have all the major veins plus some additional terminal branches and a large number of crossveins. The pronotum is large and wide, the abdomen without projecting cerci. The larvae, fig. 265, have strong biting mouthparts; elongate segmented antennae; large eyespots each composed of a group of about six facets; well-developed thoracic legs, and paired abdominal processes or gills. The apex of the abdomen has a long mesal process in Sialidae, and a pair of stout hooked larvapods in Corydalidae.

The order Megaloptera is a small one, containing only two families, the alderflies or Sialidae, and the dobsonflies or Corydalidae. Together they are represented in North America by only five genera and less than fifty species. The adults range in color from black to mottled or yellow, and in one genus (*Nigronia*) the wings are banded with black and white.

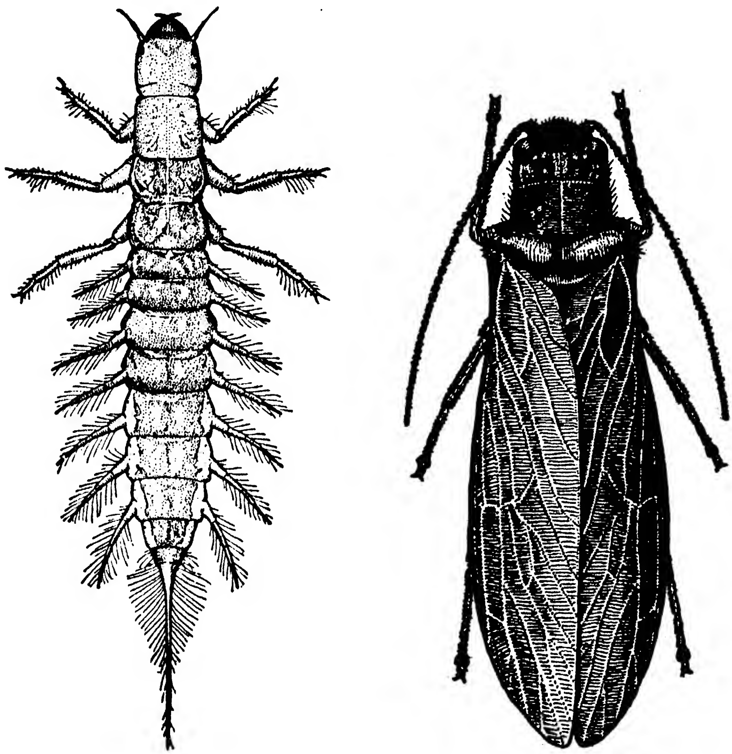

Fig. 265. An alderfly *Sialis* sp., larva and adult. (From Illinois Natural History Survey)

The larvae are aquatic, occurring in both lakes and streams. They are predaceous on small aquatic animals. The mature larvae of *Corydalus* may attain a length of 80 mm. They are ferocious larvae, highly prized for bait by fishermen, and called hellgrammites. The smaller species of the order mature in a year and have an annual life cycle. The hellgrammites require 2 or 3 years to reach full growth.

When mature, the larvae leave the water and make a pupal cell in damp earth or rotten wood near by. Here the larvae transform to pupae. Unlike those of Diptera or Lepidoptera, megalopteran pupae are active if irritated and capable of considerable locomotion. The pupal stage usually lasts about 2 weeks.

The adults are good fliers, but not agile compared to some of the flies and moths. Some *Corydalus* adults may have a wing span of 5 inches and are among our largest North American insects. The females lay their eggs in large clusters of several hundred each on stones and other objects overhanging the water. These hatch soon after deposition, and the minute larvae fall or twist their way into the water.

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Order RAPHIDIODEA

Snakeflies

Large insects, with two pairs of transparent net-veined wings, similar in many features to the Megaloptera but distinguished by the

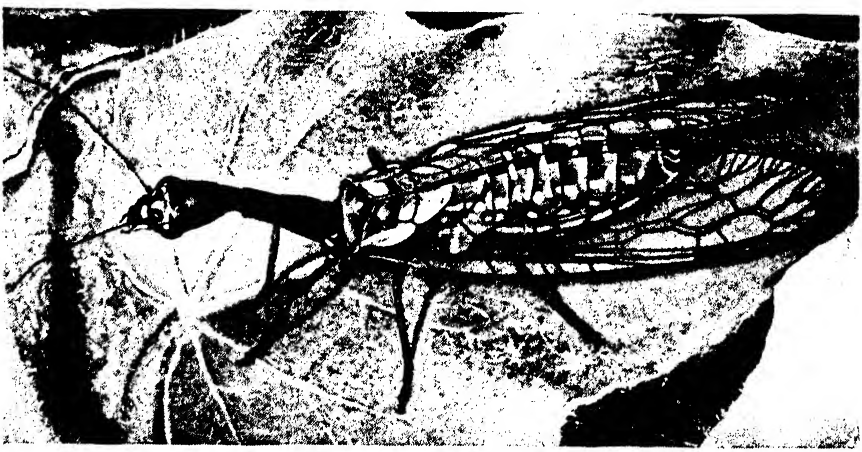

Fig. 266. A European snakefly *Rhaphidia ratzeburgi*. (From Essig, "College Entomology," by permission of The Macmillan Co.)

long serpentine neck, fig. 266. They have long antennae, chewing mouthparts, large eyes, and two pairs of very simliar wings. The female has a conspicuous terminal ovipositor. The larvae are terrestrial. They have segmented antennae, faceted eyes, well-developed thoracic legs, but no processes or appendages on the abdomen.

These queer-looking insects are confined in North America to the Rocky Mountain region. The entire known world fauna comprises only five genera and about sixty species, of which two genera and several species occur in North America. The larvae occur under loose bark of conifers and are predaceous on other insects. When mature, the larvae do not spin a cocoon but form an oval retreat in a sheltered position, and here the pupal stage is passed The adults are also predaceous. They are occasionally swept from foliage and are indeed a strange-appearing creature to find in the net.

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Order MECOPTERA

Scorpionflies

The adults, ranging in size from small to medium, either have two pairs of large net-veined wings, fig. 267, or have the wings short or

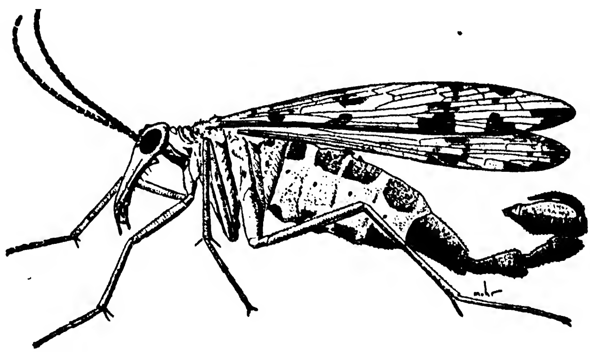


FIG. 267. A male scorpionfly *Panorpa chelata*. (From Illinois Natural History Survey)

aborted. The antennae are long; eyes large; and legs slender, in some families long and spindly. The mouthparts are of a chewing type, and are situated at the end of a snoutlike elongation of the head. The larvae are grublike or caterpillar-like, always with thoracic legs and in some groups having abdominal larvapods also, fig. 268.

The adults are omnivorous, feeding chiefly on small insects, but supplementing their diet with nectar, pollen, petals, fruits, and mosses. The winged forms are active fliers. The males of the Panorpidae, fig. 267, have a large bulbous genital capsule which resembles to some extent the abdomen of a scorpion, and from this the order derives its name "scorpionflies."

The eggs are ovoid and are laid in or on the ground, either singly or in clusters of one hundred or more. The larvae live in moss, rotten wood, or the rich mud and humus around seepage areas in densely

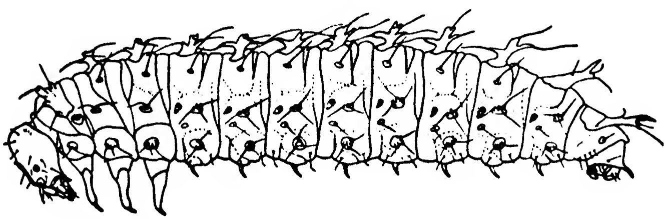


FIG. 268. Larva of *Apterobittacus apterus*. (Redrawn from Applegarth)

wooded situations. Their food consists of various types of organic matter. Pupation occurs in the soil. There is only one generation per year.

In the small species found in the genus *Boreus* the adults have small short wings and, since they mature in winter or early spring, are often found running about on the snow. These larvae live in moss and rotten wood.

REFERENCE

CARPENTER, F. M., 1931. A revision of the nearctic Mecoptera, Mus. Comp. Zool. Harv. Coll. Bull. **72**(6):206–277. 8 pls.

Order HYMENOPTERA

Sawflies, Ants, Bees, and Wasps

A large order, including many different body shapes and with a size range from 0.1 mm. in minute parasitic forms to at least 50 mm. in some of the wasps. Integument heavily sclerotized, the pleural sclerites considerably coalesced. Mouthparts are of the chewing type, in many forms modified for lapping or sucking. Wings well developed, reduced, or absent; if well developed, they are transparent, the two pairs similar in texture, and without scales; they have a great range in venation. Generalized forms, fig. 269, have a considerable reduction and coalescence of veins, but there are a moderate number of crossveins. Antennae range from 3- to about 60-segmented, and are of many shapes. Larvae are caterpillar-like or grublike, all having a distinct head and chewing mouthparts, some with thoracic or abdominal legs or both, and others without any legs.

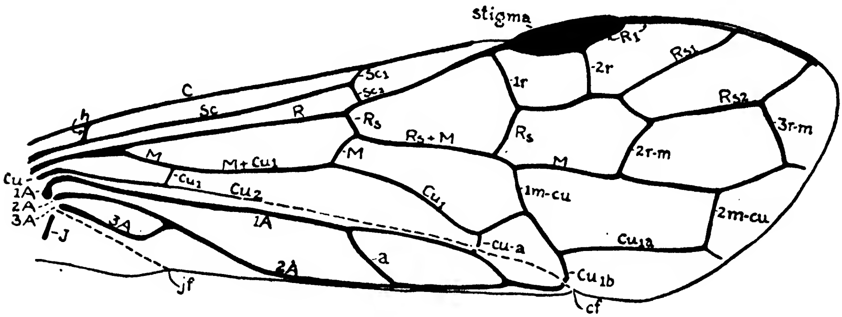


FIG. 269. Diagram of hymenopterous wing, combining primitive veins of several archaic families.

The Hymenoptera include leaf-feeding forms, parasites, predators, gall makers, and pollen feeders. In one group of families, the Apocrita, social life has been developed, carried to its highest level in the ants.

KEY TO SUBORDERS AND COMMON FAMILIES

1. First abdominal segment solidly joined with second, at most a shallow constriction between them, first tergite forming a distinct plate or pair of plates, fig. 270*A*, *B* (suborder **Symphyta**) 2

   Juncture of first and second abdominal segments constricted to form a ball-and-socket joint, fig. 270*D*; the first tergite is fused solidly to the thorax, and the remainder of the abdomen forms an articulating unit called the gaster (suborder **Apocrita**) 9

2. Antenna 3-segmented, fig. 271*A*, the third sometimes split longitudinally to form a lyre-shaped prong, fig. 271*B* . . . . **Argidae**

   Antenna at least 6-segmented, the end segment never cleft, fig. 271*C–I* 3

3. Third antennal segment at least as long as combined length of the succeeding 9 segments, the segments beyond the third forming a slender terminal filament, fig. 271*E* . . . . **Xyelidae**

   Third antennal segment not longer than the combined length of the next 3 or 4 segments, or antenna clavate, fig. 271*C* 4

4. Antenna capitate, fig. 271*C*; lateral edge of abdomen sharp and angular; large robust species, fig. 273 . . . . **Cimbicidae**

   Antenna pectinate, serrate, filiform, or in a few species as clavate as fig. 271*G*; lateral edge of abdomen round 5

5. A shallow but distinct constriction between first and second abdominal tergites, and cenchri absent, fig. 270*B* .... **Cephidae**
No constriction between first and second abdominal tergites, and cenchri (*c*) well developed, forming a pair of velvety pads, fig. 270*A* 6

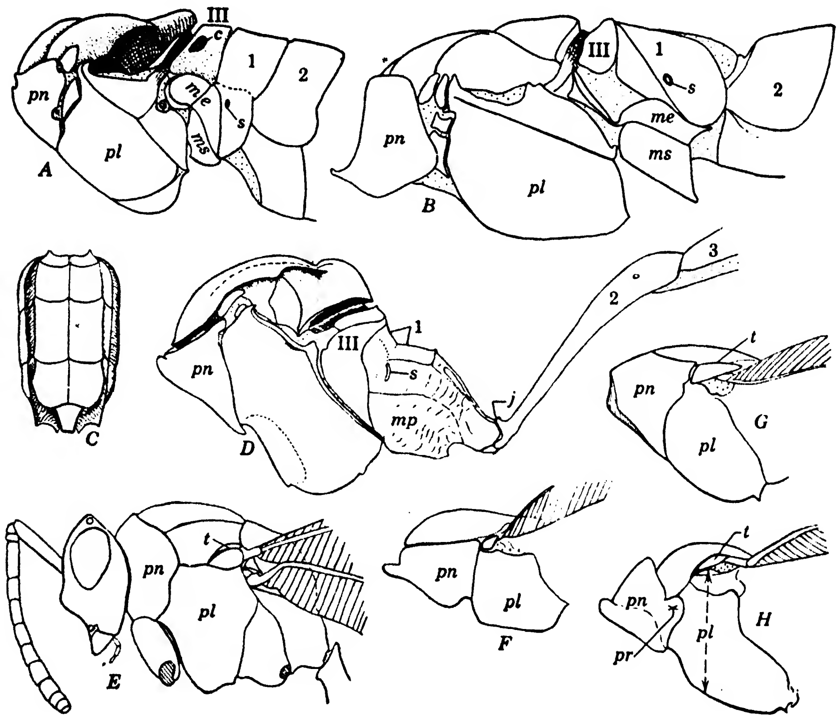


FIG. 270. Diagnostic characters of Hymenoptera. *A*, thorax of *Arge*, Argidae; *B*, thorax of *Janus*, Cephidae; *C*, venter of abdomen of *Chrysis*, Chrysididae; *D*, thorax of *Eremotylus*, Ichneumonidae; *E*, head and thorax of *Chalcis*, Chalcididae; *F*, thorax of *Proctotrupes*, Proctotrupidae; *G*, thorax of *Ancistrocerus*, Vespidae; *H*, thorax of *Sceliphron*, Sphecidae. *c*, cenchrus; *j*, basal articulation of gaster; *me*, metaepimeron; *mp*, metapleuron; *ms*, metaepisternum; *pl*, mesopleura; *pn*, pronotum; *pr*, pronotal lobe; *s*, first abdominal spiracle; *t*, tegula. III, metanotum. 1, 2, 3, segments of abdomen.

6. Front tibia having only one apical spur .... **Siricidae,** p. 320
Front tibia having two apical spurs 7
7. Antenna 7- to 9-segmented, fig. 271*F–H* .... **Tenthredinidae,** p. 319
Antenna having 10 or more segments, figs. 271*D*, *I* 8
8. Antenna narrow and filiform, proportioned as in fig. 271*H*
Tenthredinidae, p. 319
Antenna serrate in females, fig. 271*D*, pectinate in males, fig. 271*I*
Diprionidae, p. 319

9. Petiole composed of two segments, usually one or both bearing a dorsal hump or node, fig. 285 .... **Formicidae,** p. 327
Petiole consisting of only one segment, figs. 286, 287 10
10. First segment of gaster forming an isolated petiole bearing a dorsal node or projection, fig. 286; includes winged and wingless forms. . **Formicidae,** p. 327
First segment of gaster either expanded posteriorly or not bearing a dorsal node 11
11. Wings completely atrophied or reduced to small pads 12
Wings well developed, reaching to or beyond middle of abdomen 13

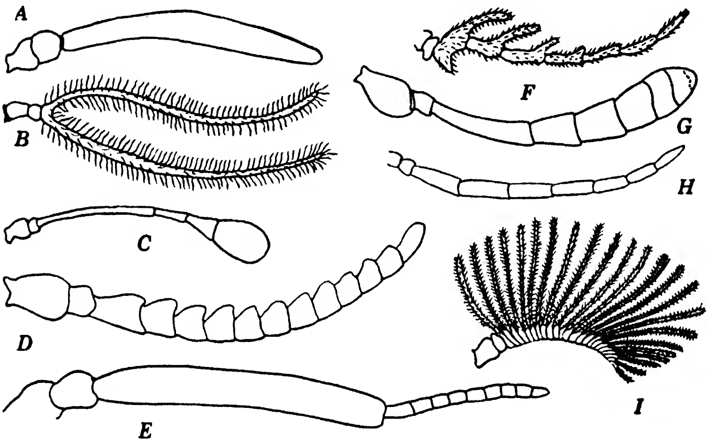


FIG. 271. Antennae of Hymenoptera. *A, Sofus* female, Argidae; *B, Sphacophilus* male, Argidae; *C, Trichiosoma,* Cimbicidae; *D, Augomonoctenus* female, Diprionidae; *E, Pleroneura,* Xyelidae; *F, Cladius,* Tenthredinidae; *G, Tenthredo,* Tenthredinidae; *H, Pseudodineura,* Tenthredinidae; *I, Monoctenus* male, Diprionidae.

12. Body fuzzy with dense hair, fig. 282 .... **Mutillidae,** p. 325
Body smooth or with only inconspicuous hair. A few species in each of several families of parasitic habit, keyed no further here.
13. Front wing without a stigma (a thickened area along the anterior margin of the wing), and with sclerotized venation reduced to a single anterior vein, sometimes with a "tail" at its tip, fig. 272*D*, sometimes completely atrophied 14
Front wing either having a definite stigma or having a more extensive venation, fig. 272*F* 15
14. Lateral corner of pronotum extending to the tegula, fig. 270*F*. Several families of small parasitic wasps, chiefly .... **Proctotrupoidea**
Lateral corner of pronotum not extending to the tegula, fig. 270*E* **Chalcidoidea,** p. 322
15. Pronotum having each posterolateral corner forming a round lobe which does not reach tegula, fig. 270*H* 16
Pronotum having posterolateral corner truncate or angulate, practically touching the tegula, fig. 270*G* 17

16. Body and appendages without branched hairs, each hair simple, neither branched nor fringed . . . . **Sphecoidea,** p. 330

Body and appendages having branched or spiral hairs; each hair has many branches or whorls and may appear fringed, fig. 289 . . . . **Apoidea,** p. 331

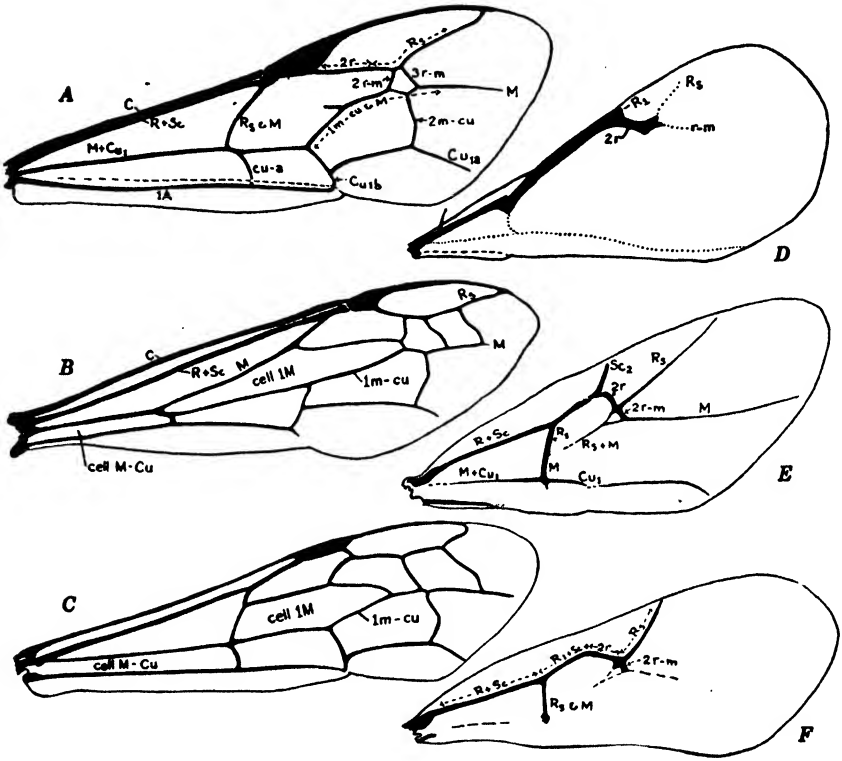


Fig. 272. Wings of Hymenoptera. *A*, Ichneumonidae; *B*, *Vespa*, Vespidae; *C*, *Myzine*, Tiphiidae; *D*, *Tetrastichus*, Chalcididae; *E* and *F*, two types of Cynipidae.

17. Front wing having costa and stem of radius united, obliterating the costal cell, fig. 272*A* 18

Front wing with an open costal cell between radius and costa, fig. 272*B*, *C* . . 19

18. Front wing having crossvein 2*m-cu*, fig. 272*A* . . . . **Ichneumonidae,** p. 321

Front wing lacking crossvein 2*m-cu* . . . . **Braconidae,** p. 322

19. Sternites of abdomen very hard and concave, the three large ones divided by a linear mesal ridge into three pairs of large armored plates metallic in appearance, fig. 270*C*. Robust, hard, shining, metallic bees capable of curling up into a ball . . . . **Chrysididae**

Venter of abdomen usually convex, its sternites not divided into paired armored plates 20

20. Front wings having no definite stigma, but instead a clear, triangular area bounded posteriorly by a vein, fig. 272*E, F,* but without an anterior vein **Cynipoidea,** p. 323
Front wings having a thickened stigma, fig. 272*B, C,* or an anterior vein.....21

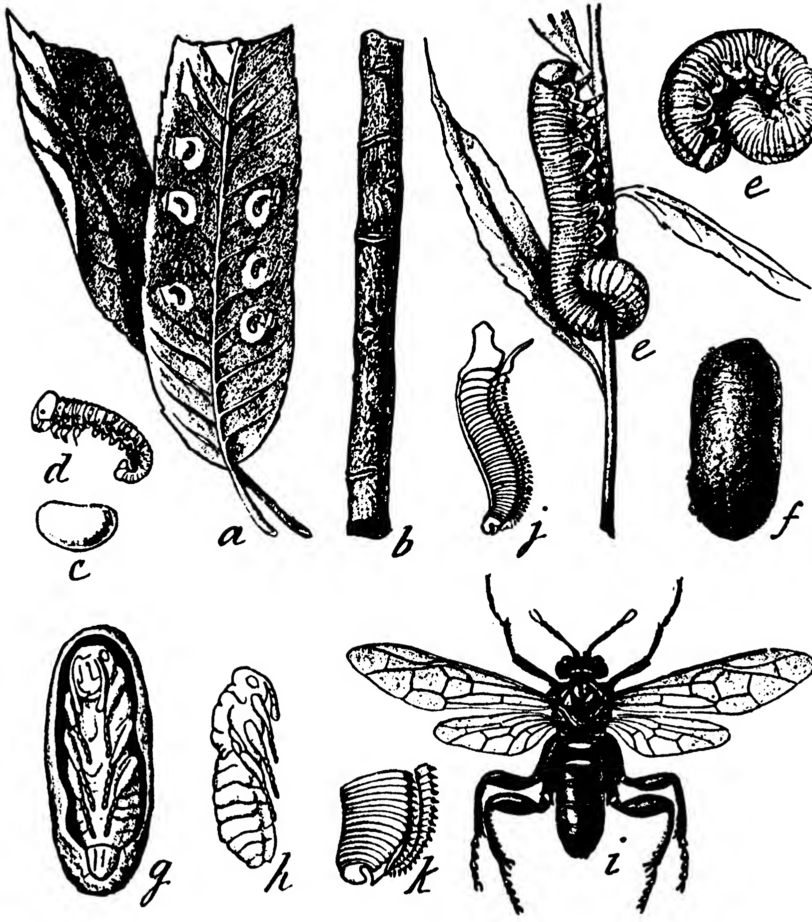


FIG. 273. A large sawfly *Cimbex americana.* *a,* willow leaves showing location of eggs; *b,* twig showing incisions made by adult; *c,* egg; *d,* newly hatched larva; *e, e,* mature larvae; *f,* cocoon; *g,* open cocoon showing pupa; *h,* pupa, side view; *i,* mature sawfly; *j, k,* saw of female. (After Riley)

21. Front wing having cell 1*M* longer than cell *M-Cu,* fig. 272*B;* wings pleated lengthwise when folded..................................**Vespidae,** p. 325
Front wing having cell 1*M* shorter than cell *M-Cu,* fig. 272*C,* or former cell open due to atrophy of 1st *m-cu.* Several closely related families of parasitic wasps, including..................**Mutillidae, Scoliidae, Tiphiidae,** p. 325

Suborder SYMPHYTA

Sawflies and Horntails

The symphyta, with the exception of the small parasitic family Orussidae, are a plant-feeding group. The larvae either feed externally on foliage or mine in leaves, leaf petioles, or stems. The adults of many groups feed on the pubescence of the host plant, cropping it by means of their sickle-shaped mandibles as a cow does grass; in other groups they may be predaceous on smaller insects or feed on nectar and pollen. The group is a large one; the North American forms represent twelve families and include in their host selection a great diversity of plant groups.

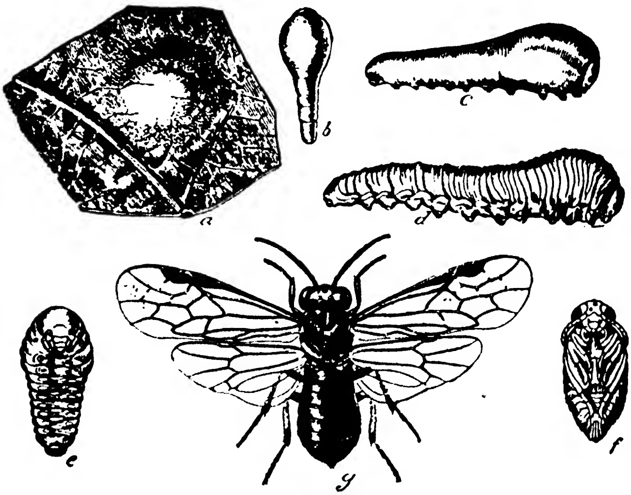


FIG. 274. The peach-slug *Caliroa amygdalina*. *a*, egg *in situ*; *b*, newly hatched larva; *c*, larva nearly full grown; *d*, larva after last molt, ready to enter ground for pupation; *e*, prepupa; *f*, pupa; *g*, adult. (From U.S.D.A., B.E.P.Q.)

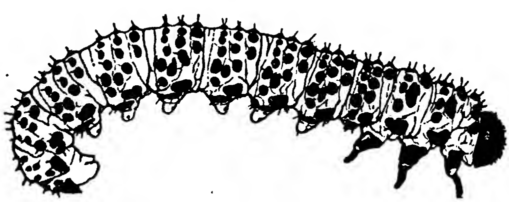


FIG. 275. The feeding stage larva of the imported currantworm *Nematus ribesii*. (From Connecticut Agricultural Experiment Station)

Distinguishing features of sawfly larvae are: a distinct head, with simple chewing mouthparts; antennae slender or platelike with one to seven segments; eyes with only a single lens; and abdominal legs (when present) without hooks or crochets.

The adults of most sawflies are compact and fairly robust. Of the leaf-feeding families, the largest common species is *Cimbex americana*, fig. 273, in which the antennae are capitate; the males and females

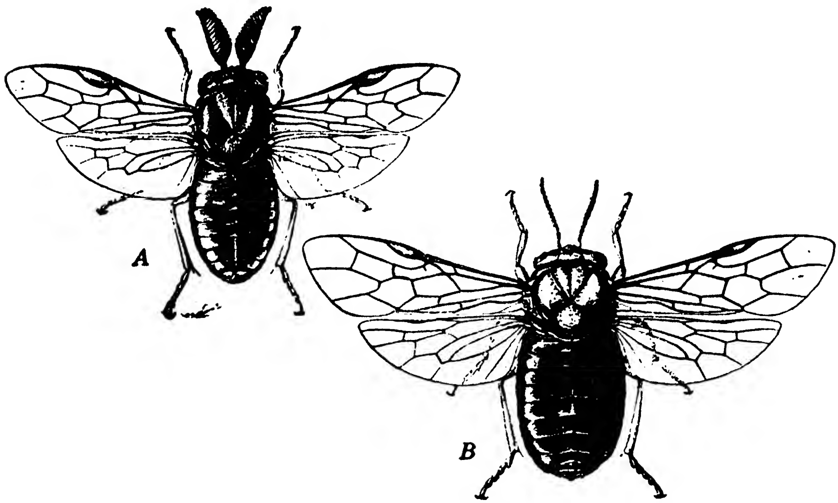


FIG. 276. Leconte's sawfly *Neodiprion lecontei*. *A*, male; *B*, female. (From U.S.D.A., B.E.P.Q.)

are differently colored. The females of all but a few species have a well-developed saw used to cut egg slits in leaves or petioles.

The Tenthredinidae is the largest family, characterized chiefly by the simple 9- to 16-segmented antennae. Most of the species are external leaf feeders, and among them are several of economic importance, such as the rose-slug *Endelomyia aethiops;* the imported currant worm *Nematus ribesii*, fig. 275; and the larch sawfly *Pristiphora erichsonii*. In certain species the larvae mine in the leaf tissue, for example, *Heterarthrus nemorata*, one of the birch leaf miners. Species of other genera, including *Euura*, produce true galls.

The Diprionidae is another economically important family. In this family the antennae are at least 13-segmented, serrate in the female and pectinate in the male, fig. 276. All the species are stout and more or less drab in color. The larvae are caterpillar-like and external feeders on coniferous needles. Many species are among the worst defoliators of spruce and pine forests. Of special note are the ravages caused to spruce in northeastern America by the European spruce sawfly *Diprion hercyniae.* Especially injurious to young pines is the common red-headed pine sawfly *Neodiprion lecontei,* fig. 276.

The Siricidae contain some of the largest members of the suborder. They are elongate, sometimes attaining a body length of 40 mm.

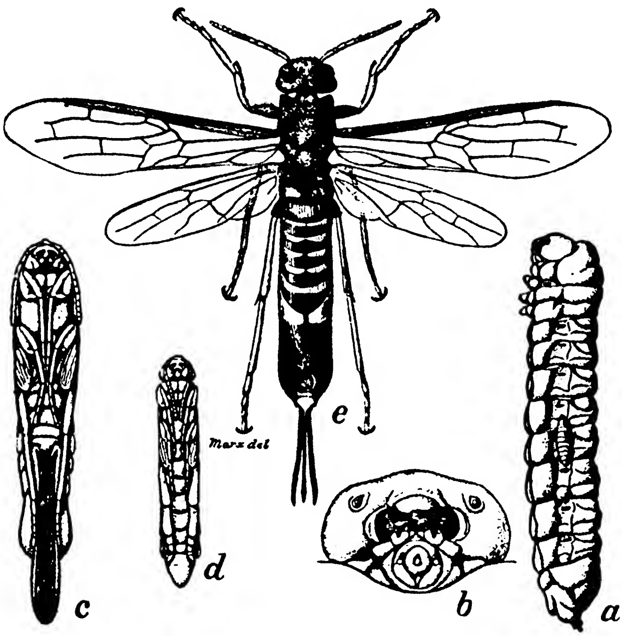


Fig. 277. A horntail wasp *Tremex columba.* *a,* larva; *b,* larval head, ventral aspect; *c, d,* female and male pupa; *e,* adult. Note small parasite larva attached to horntail larva. (After Riley)

The larvae bore in tree trunks and are round and almost legless. Both adults and larvae have a horny spikelike projection at the posterior end of the body, the character which gives them the name "horntails." *Tremex columba,* fig. 277, is a common species attacking maple, elm, beech, oak, and some other deciduous trees.

Suborder APOCRITA

Ants, Bees, and Wasps

In general the Apocrita are more graceful, active, and more rapid of movement than the Symphyta. The larvae are chiefly internal or external parasites, or are fed by the adults, or make plant galls. They are legless, have a distinct exposed head capsule bearing greatly reduced mouthparts and antennae, and frequently exhibit hypermetamorphosis.

In the Apocrita the first segment belonging to the abdomen is fused solidly with the thorax, so that what appears to be the abdomen really has lost its anterior segment. This body region which appears to be the abdomen is termed the *gaster.*

Ichneumonidae, the Ichneumon Flies. Usually slender wasps, having long and many-segmented antennae, fig. 278, and having subcosta

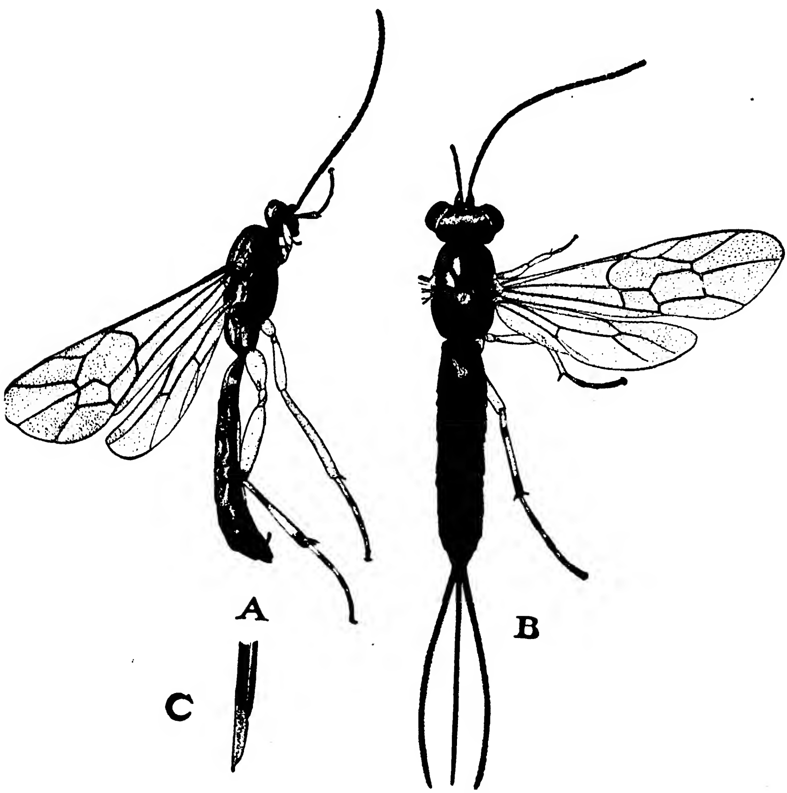


FIG. 278. An ichneumon wasp *Glypta rufiscutellaris. A,* male; *B,* female; *C,* tip of ovipositor. (From Connecticut Agricultural Experiment Station)

fused with the stem of radius in the front wings. All members of this family are parasites on insects or spiders. Their favorite hosts are the larvae of Lepidoptera, for example, *Glypta rufiscutellaris,* a parasite of the oriental peach moth. In addition, a number of ichneumon flies parasitize the larvae of Coleoptera, Hymenoptera, and Diptera, and a few other insects. The adult ichneumon fly female deposits its eggs on or inside the body of the host. If the eggs are laid on the epidermis of the host, the newly hatched larvae may bore into the body. The larvae develop into legless grubs which either attach to the outside of the host or develop within the body of the host. When mature, the larvae spin pupal cocoons near the host; the grubs may pupate within the host or leave it to spin cocoons. Ichneumon flies have a wide range in size. Many of the small forms only a few millimeters long parasitize small moth larvae.

Braconidae. This is a large family closely related to the ichneumon flies. The species average smaller than the ichneumon flies, and many braconids have reduced wing venation. A number of species are important as parasites of economic pests. One of these, *Apanteles melanoscelus,* fig. 175, has been imported for biological control of gypsy-moth larvae. This small parasite exhibits the interesting hypermetamorphosis prevalent among most of the parasitic families of Hymenoptera. In fig. 175 are illustrated the different shapes of the larva in various stages of development; the anal vescicle (*a*) may be used to identify the posterior end of the larva.

Superfamily Chalcidoidea, the Chalcid Flies. Small wasps, sometimes less than a millimeter in length, having a greatly reduced wing vena-

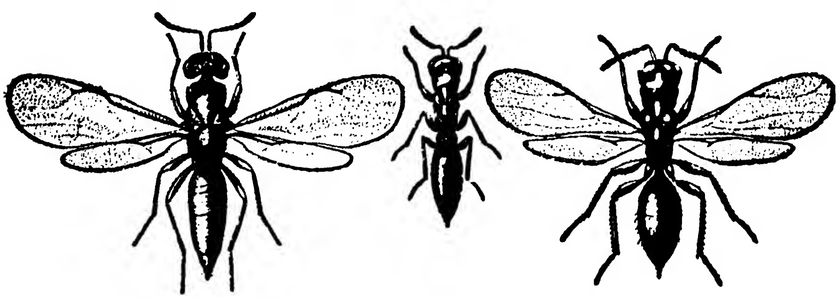


FIG. 279. *A,* the wheat jointworm *Harmolita tritici,* and *B,* wingless and winged forms of the wheat strawworm *Harmolita grandis.* (From U.S.D.A., B.E.P.Q.)

tion, fig. 279, and usually having elbowed antennae. These wasps are largely internal parasites, especially of larval Lepidoptera and of the larvae of other parasitic Hymenoptera, which they attack within the body of the primary host. These parasites of parasites are called hyperparasites. The few chalcids which are not parasitic develop in various seeds, or in plant stems, especially grasses. To this non-parasitic group belongs the clover-seed chalcid *Bruchophagus gibbus,* whose larva develops in the seeds of clover and alfalfa; the wheat jointworm *Harmolita tritici,* whose larva bores in the stems of wheat; and the wheat straw-worm *Harmolita grandis,* fig. 279. Locally and sporadically the wheat jointworm causes serious damage to the crop.

Of unique interest is the specialized life history of certain tiny chalcid flies belonging to the family Agaontidae. These develop in the seeds of figs. The males are wingless and live only within the fig fruit in which they develop, fertilizing the females even before the latter emerge from the fig seed. The females are winged and fly from flower to flower in search of suitable seeds for oviposition, carrying the pollen on their bodies and pollinating each flower visited. This is the only method by which figs are pollinated. Many commercial varieties of figs do not require pollination to develop their fruits, but the fruit of the choice Smyrna fig will not develop without pollination. In order to grow these in North America it was necessary to introduce the European fig chalcid *Blastophaga psenes* to effect pollination.

Superfamily Cynipoidea, the Gall Wasps. These are small wasps, most of them characterized by the large triangular cell near the stigma

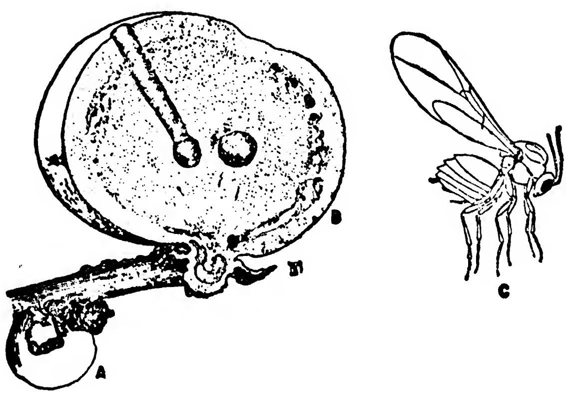


Fig. 280. A cynipid, *C*, and its gall; *A*, immature gall, and *B*, a section of mature gall showing cells and exits. (From Essig, "College Entomology," by permission of The Macmillan Co.)

of the front wing, fig. 272, and by the deep but bilaterally compressed abdomen. Many groups of the superfamily are parasitic on dipterous larvae, aphids, and other insects, but the best-known group produces galls on plants. As a matter of fact, the gall wasps themselves are seldom seen, but every naturalist is familiar with some of the many different types of galls that are produced on the leaves, stems, or roots of oak, roses, and other plants by the larvae of these insects. One of these is shown in fig. 280. There are hundreds of species of gall wasps, nearly every species producing a different type of gall. Some species which live on oaks have an alternation of generations, with one generation producing a gall on the roots and the alternate generation making a gall on the leaves or twigs.

Provisioning and Social Wasps and Bees

These insects are of special interest because social life has been developed independently in three groups. An account of the development of the social habit is given in Chapter 6. Most of the families, however, are solitary, and parasitic, predatory, or pollen feeding in habit.

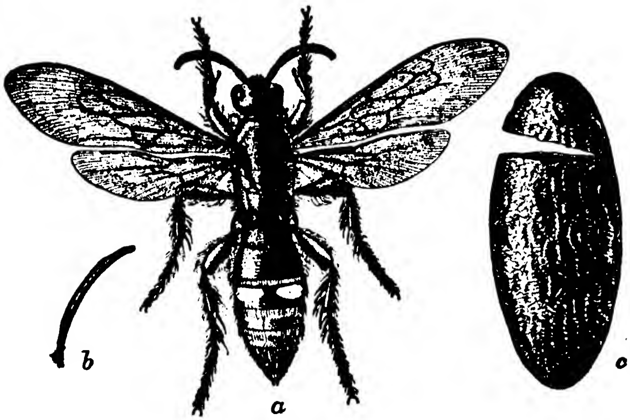


FIG. 281. A digger wasp *Discolia dubia*. *a*, female wasp; *b*, antenna of male; *c*, cocoon showing escape opening. (From U.S.D.A., B.E.P.Q.)

Most of the non-social wasps secrete a remarkable substance that is discharged with their sting. When injected into their prey, this secretion causes complete motor paralysis without death resulting. Such a paralysis is used by wasps that lay an egg on the prey or provision a nest with prey. The induced paralysis has a triple advantage: It keeps the prey edible until the wasp larva hatches and begins feeding, it insures that the prey will not move away from the legless wasp larva, and it prevents the attraction of scavenger insects to the odor of dead insects.

Scoliidae, the Scoliid or Digger Wasps. These fairly large insects have wings in both sexes, and most of the species are black or are banded or spotted with black and yellow, such as *Discolia dubia,* fig. 281. The female wasps dig through the soil in search of their prey, white grubs (larvae of the beetle family Scarabeidae). When the female encounters a suitable host larva, she stings it, thereby paralyzing it; digs a crude cell around it; lays an egg on the doomed larva; and then moves on in search of another victim. The egg soon hatches into a legless grub which attaches to the paralyzed beetle larva and begins eating it. Within a period of about 2 weeks, the wasp larva has consumed the host and is full grown. It then spins a cocoon in the earthen cell and usually passes the winter in this stage. The next spring or summer the larva pupates, and later the adult chews its way out of the cocoon and digs to the surface.

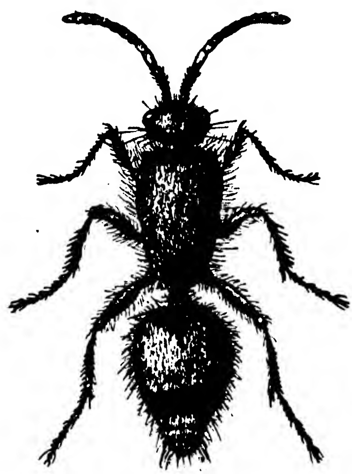


FIG. 282. A mutillid wasp female *Dasymutilla ferrugata.* (After Washburn)

Closely related to the scoliid wasps are many families of somewhat similar habits. Species of the family Mutillidae are parasites of wasps and bees. In many mutillids the females are wingless and have a close resemblance to ants. The Mutillidae females, however, lack the "node" on the petiole of the gaster, fig. 282, and in addition are covered with dense velvety or silky pile. From this latter character the family has received the name velvet ants. These velvet ants have a powerful sting and use it freely if interfered with.

Many oriental species of *Tiphia,* of the related family Tiphiidae, have been brought to the United States and propagated for parasitizing grubs of the Japanese beetle, and a few have shown definite promise of assisting in the control of the beetle.

Vespidae, Yellow Jackets and Hornets, Wasps. This family contains species varying from 10 to about 30 mm. in length, many of them having elaborate yellow and black or white and black markings.

fig. 283. They differ from other members of the Aculeata in that the wings in repose are folded longitudinally like a fan. Most of the Vespidae are solitary in habit. The adults make a burrow in wood or soil or construct a pottery container for the abode of the grub. The nest is usually stocked by the adult with paralyzed caterpillars or with pollen and honey. Certain of the Vespidae are social in habit. By masticating wood fibers with an oral secretion, they produce a paper which they fashion into a platelike or baglike nest. The most

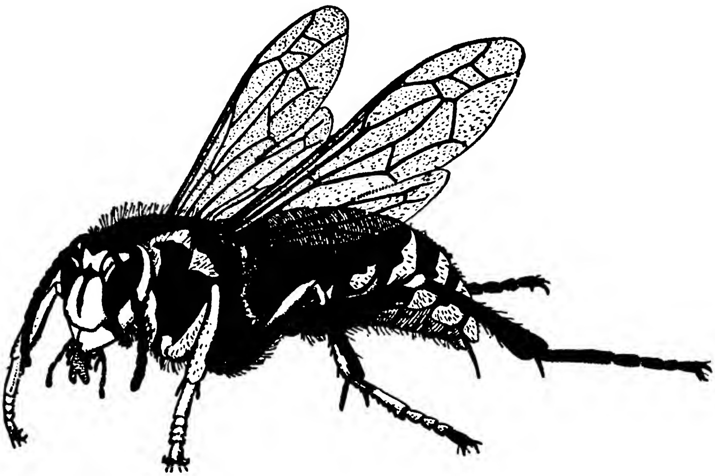


FIG. 283. The bald-faced hornet *Vespa maculata*. (From Illinois Natural History Survey)

familiar of these are the platelike nests of *Polistes*, fig. 284, which are made up of a single horizontal comb of larval cells. These are commonly found hanging from eaves of buildings and in similar sheltered places. Colonies of *Polistes* rarely have over a few dozen members. The largest colonies of vespids found in North America are made by the bald-faced hornet *Vespa maculata*. These colonial nests, oval in shape and with an opening at the bottom, are most often attached to tree branches. Each contains several layers of larval cells, or combs, arranged one above the other. The workers in a colony forage for insect prey, such as flies and caterpillars. These are crushed and mangled by the wasps and fed to the maggot-like larvae in the cells of the nest.

In temperate regions of North America the colonies die out at the end of autumn. In late summer a brood of males and females is produced. At frost the workers and males die; the autumn brood of females, by this time fertilized, hibernate in rotten logs or stumps. These females emerge the following spring and begin new colonies.

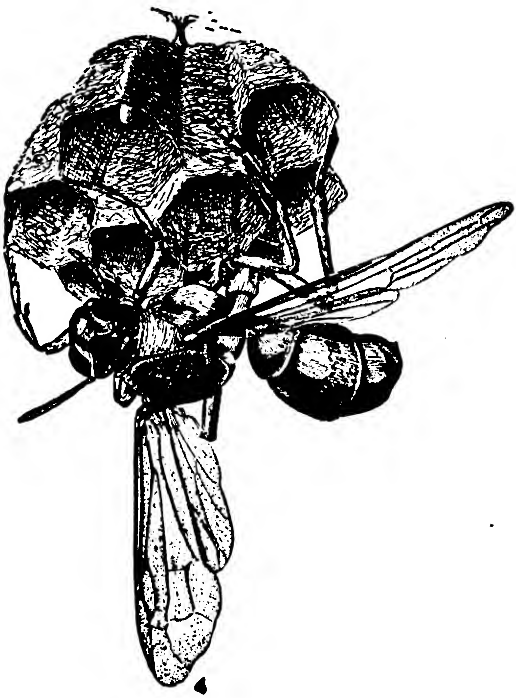


FIG. 284. Adult queen and nest of *Polistes*. (From U.S.D.A., B.E.P.Q.)

Formicidae, Ants. In these insects the first segment of the gaster forms a petiole or stalk and bears a dorsal projection or node, figs. 285, 286. This structure differentiates ants from other antlike wasps. In addition to the normal males and females, ant species usually have a third form, the non-reproductive workers, which are always wingless. These workers are the ants we usually see scurrying about. They perform most of the work of the colony, such as building the nest, excavating the subterranean chambers, and gathering food for the colony.

A typical colony starts with the swarming flights of the winged reproductive males and females. At periodic intervals (frequently once a year) large numbers of winged males and females are produced in an established colony. When weather conditions are favorable, the sexual forms leave the nest as a swarm, embark on their nuptial flight, and mate in flight. The male dies soon after mating. The fertilized female seeks a suitable nest site in the ground, an old log, or other situation, bites off her wings, and seals up a small hollow, which becomes the first nest chamber. The female remains in this chamber for several weeks, during which time the eggs are laid and the grublike larvae are fed to maturity by the female. The food is

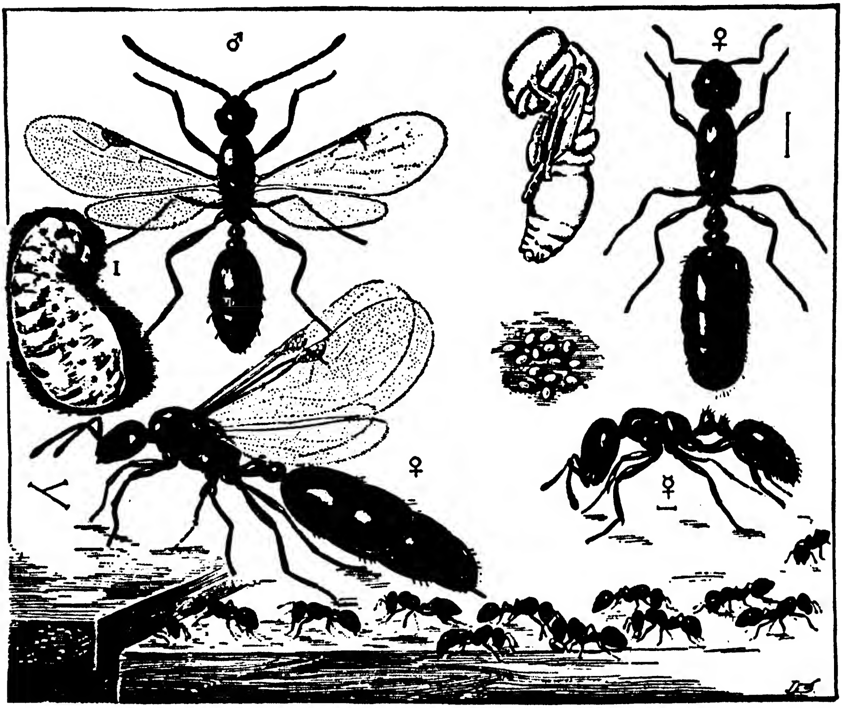


FIG. 285. The little black ant *Monomorium minimum,* showing several stages and activities. (After Marlatt, U.S.D.A., B.E.P.Q.)

produced apparently from the histolysis of the wing muscles and the fat body of the female. It is extruded from her mouth as a secretion. The mature larvae pupate and soon emerge as small workers. These break out of the nest chamber, seek food, and henceforth keep the female, or queen, and the next brood of workers provided with food. Subsequent broods help with the task of keeping the colony provisioned. The female continues to lay eggs, without further fertilization, for several years.

Colonies of many species contain only a few dozen or a few hundred individuals, whereas those of other species may attain a population of many thousands. The small colonies are usually situated under stones, in stumps, logs, or in galleries in the soil. Many of the large colonies build large mounds of earth, sticks, and debris, interspersed with a complex system of galleries and chambers.

In the main, ants are omnivorous, feeding on living or dead animal matter (especially other insects), vegetable substances such as fungi, and sweet exudates or secretions of plants, such as honeydew, nectar, wound discharges, and glandular products. Certain insects such as

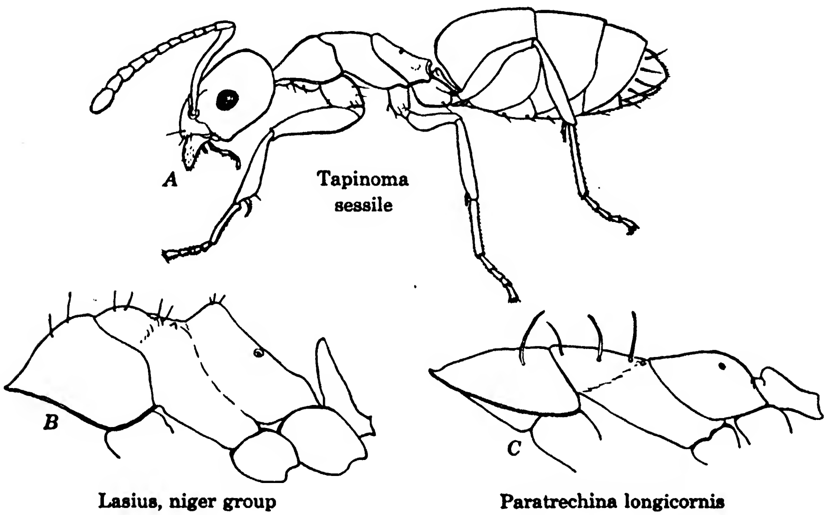


FIG. 286. Lateral aspect of three ant genera to illustrate the dorsal node on the petiole. Note that in *A* this node is small but distinct.

aphids and some scale insects produce honeydew or other secretions; the ants tend these insects with great care and "harvest" the sweet substances produced. Some ant species are extremely savage and live almost entirely by the capture of live insect prey. Others live almost entirely on sweets, fats, or dead insects.

Several ant species invade houses or stores and are among the most persistent domestic pests. In the northern states the thief ant *Solenopsis molesta,* Pharaoh ant *Monomorium pharaonis,* and the odorous house ant *Tapinoma sessile* are common household species. In the southern states the introduced Argentine ant *Iridomyrmex humilis* is an exceedingly common household pest and has almost replaced the native ant population in many localities.

Some of the ants feed primarily on plant seeds. Of these ants, various species of the genus *Pogonomyrmex,* known as "agricultural ants," have become abundant and are destructive in the grain and grass areas of the Great Plains and westward.

Superfamily Sphecoidea, the Solitary Wasps. These insects are characterized by the shape of the pronotum: Each corner ends in a small round lobe that is situated beneath but does not touch the tegula,

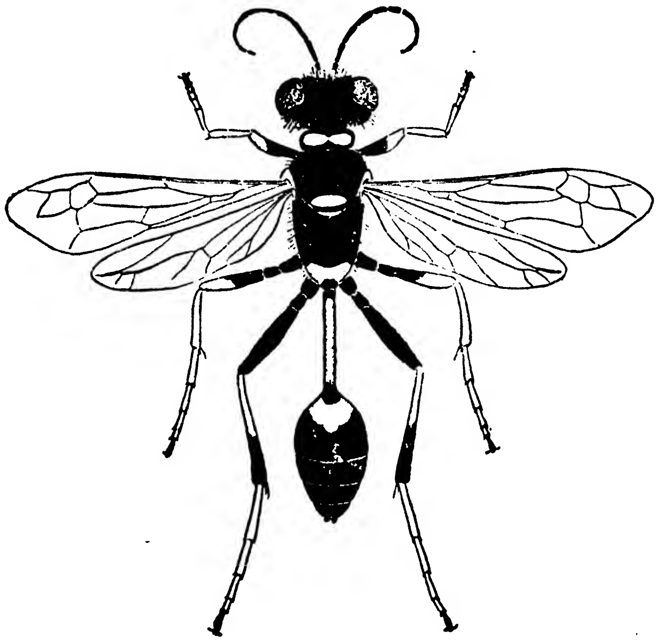


FIG. 287. The y and black mud dauber wasp, *Sceliphron servillei,* that builds series of mud ce. on stones and walls and provisions them with spiders. (From Essig, "Insects of Western North America," by permission of The Macmillan Co.)

fig. 270*H*. In addition, the hair is simple and undivided, in contrast to that of the bees. The group is a large one and includes a great diversity of sizes, shapes, and colors. The habits of all members are essentially the same. The female wasp makes a mud nest or a nest excavated in pith, wood, or soil and provisions it with a particular kind of paralyzed prey. An egg is deposited in each stocked compartment of the nest, this egg hatching into a legless grub which feeds on the provender stored for it by the parent. In temperate climates the larva overwinters in its cocoon, pupating the following year in early summer.

The various wasp groups are usually specific in the prey they choose for provisioning the larval cells. The Pemphredoninae (often only

2 or 3 mm. long) capture aphids, the Sphecinae usually use caterpillars, the Trypoxylinae use spiders, and so on. One of the most interesting and showy species in the central and eastern states is the cicada killer *Sphecius speciosus.* This is a large black and yellow species which attains a length of 40 or 50 mm. It commonly captures and paralyzes the common cicada *Tibicen linnei* and carries it to a burrow in the ground, provisioning each burrow with one cicada. When attacked by the wasp, the cicada makes a loud piercing noise, but this subsides in a moment as the cicada is stung and becomes paralyzed.

The most familiar of the solitary wasps are the thread-waisted mud daubers, especially species of *Sceliphron,* fig. 287. These mud daubers build a mud nest of several cells. The nests are common under bridges, eaves of houses, or other sheltered places. The wasps gather the mud at the edge of near-by pools or puddles, flying back and forth from water's edge to nest with mouthfuls of "plaster." The cells are provisioned with spiders.

Superfamily Apoidea, the Bees. This group, fig. 288, includes all the native and domestic bees. They are very similar morphologically

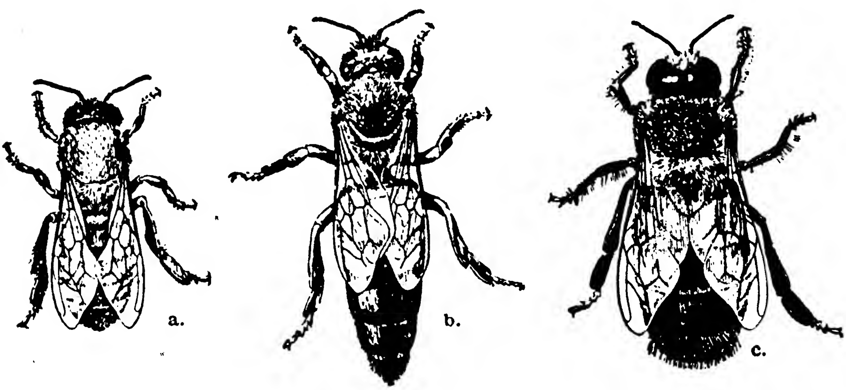


FIG. 288. The honeybee. *a,* worker; *b,* queen; *c,* drone. (From U.S.D.A., B.E.P.Q.)

to the Sphecidae, possessing the same characteristic round lobe at the corner of the pronotum. The bees differ in having branched body hairs, fig. 289, which give them a fuzzy or velvety appearance. Most of our thousand or more species are solitary in habit, making cells in burrows or cavities as do many solitary wasps. The bees provision the nest cells with honey and pollen, which constitutes the food of the larvae. Certain genera of bees are "parasitic," laying their eggs in the cells or nests of other bees. The intruder larva matures faster than the host larva and eats up the stored food. These "parasitic" bees could be called "cowbird bees."

Of our native fauna the bumblebees alone have developed social living. In this group fertilized females overwinter in log cavities or ground cover. They emerge in spring, find a protected site in a hole in the ground or in a deserted mouse nest, and begin a colony. A

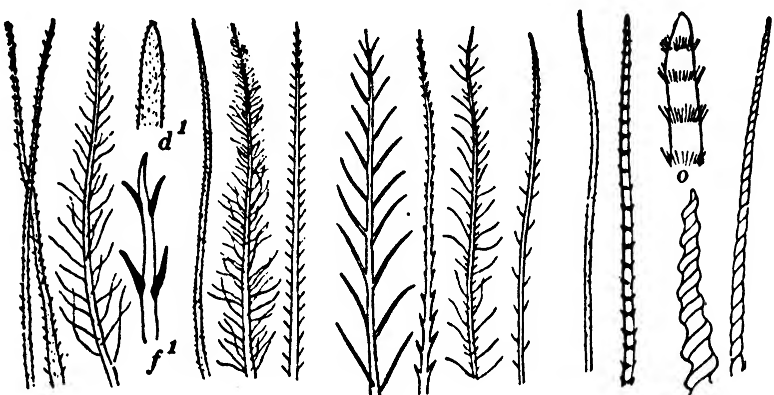


Fig. 289. Hairs of bees. (After J. B. Smith)

brood of eggs and young is raised, the mother, or queen, feeding the larvae on honey. This brood is composed of sterile females or workers that take over the task of gathering food for succeeding larvae. Toward fall no more workers are produced, but instead a swarm of males and functional females. The males die soon after mating, and the workers also die at the approach of winter. The new brood of fertilized queens disperses for hibernation, and the entire colony is disbanded.

The habits of the domestic honeybee *Apis mellifera* are much more specialized than those of the bumblebee. In the first place the colonies do not die out during the winter; their members live during this period on honey stored up throughout the summer. Individual queens have lost the ability to forage for themselves; hence they cannot start a new colony alone but must be accompanied by some workers from the parent colony. The phenomenon of "swarming" is the colonization flight in which the new queens set out to form a new nest.

The honeybee is of considerable importance in that it affords a large cash return from the sale of honey. But the greatest role of the bees is the pollination of a great variety of wild and domestic plants, including most of our commercial fruits and legume crops.

Reference

Viereck, et al., 1916. The Hymenoptera of Connecticut, Conn. Geol. Nat. Hist. Surv. Bull. **22**:824 pp. 10 pls., 15 figs.

Order COLEOPTERA

Beetles and Weevils

The adults usually have two pairs of wings: The first pair is veinless, hard, and shell-like, and folds together over the back to make a stout wing cover; the second pair, used for flight, is membranous,

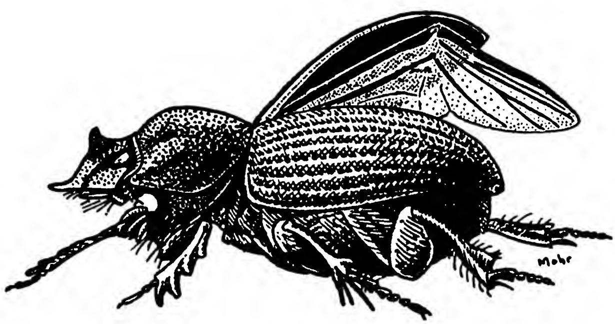


Fig. 290. A stag beetle *Copris minutus*. (From Illinois Natural History Survey)

usually veined, and in repose folds up under the wing covers or elytra, fig. 290. The body is normally hard and compact. The mouthparts are of the chewing type; the antennae are well developed, usually 10- to 14-segmented; the compound eyes are usually conspicuous; and the legs are heavily sclerotized. The larvae, fig. 297, normally have distinct head capsules, chewing mouthparts, antennae, and thoracic legs, but no abdominal legs. The pupae, fig. 305, have the adult appendages folded against but not fused with the body.

The Coleoptera comprise the largest order of the Insecta. There are about twenty-five thousand species in North America, representing about one hundred and fifty families. The adults vary in size from less than a millimeter long to several inches (up to 100 mm.). The shape and coloring varies just as much, but the most brilliantly colored, weird-shaped, and gigantic species occur in the tropical regions of the world.

Most of the beetles are either plant feeders or are predaceous on other insects. Usually both adults and larvae of the same species have similar food habits; that is, both forms will be phytophagus, or both will be predaceous, although the larva may not feed on either the same species of plant or the same part of the plant. Thus the June beetles which are phytophagous utilize different parts of plants for food during their development. The adults feed on the foliage of forest trees, but the larvae, known as white grubs, feed on the roots of trees, shrubs, herbs, or grasses. The predaceous beetles are active hunters, stalking their prey. Certain groups have more specialized food habits. Some are endoparasites of other insects or feed on insect egg masses.

The order as a whole is terrestrial. Certain families, however, are aquatic, both larvae and adults living in water. The larvae usually leave the water to pupate, making an earthen cell in near-by soil. As is the case with the land forms, the aquatic group includes both herbivorous and predaceous species, the latter predominating.

The great majority of beetles have a single generation per year and a simple life cycle similar to the following. The oval or round eggs are laid in spring or early summer and hatch in 1 or 2 weeks. The larvae are voracious feeders, usually attaining full growth during the summer and pupating in the soil. The adults emerge in a few weeks, feeding and maturing throughout the remainder of the summer and autumn. With the advent of cold weather they hibernate. The following spring these adults emerge and lay eggs, and the cycle begins again. The old adults usually die soon after egg laying is completed.

There are many deviations from this biological pattern. For example, some ladybird beetles have continuous and overlapping generations throughout the warmer seasons. In other groups, notably many species whose larvae live in soil or rotten wood, the winter is passed in the larval stage, and the adults occur for only a limited span during spring or summer.

Synopsis of Suborders

1. Males having finger-like elytra which are held out from the sides of the body; hind wings large, folding only fanwise; metanotum greatly enlarged. Females wingless; in some families the female is only a sac partly protruding from the host tissue; in others free living, but larviform in appearance.... **Strepsiptera**

Males having elytra wider and folded over back in repose; hind wings either absent or folding in several directions; metanotum much smaller. Female similar to male in general appearance except in a few rare cases..........2

2. First sclerotized sternite of abdomen completely divided by posterior coxae into two or three separated parts, two lateral sclerites, and sometimes a small mesal sclerite between the bases of the metacoxae, fig. 291(1)....**Adephaga**

First sclerotized sternite of abdomen forming a complete band from one side to the other; the posterior coxae may extend over and above this band, but the sclerite itself is intact underneath them, fig. 291(2)........................3

3. Head with two ventral gular sutures forming a gula; anterior portion of head not prolonged to form a beak; the mouthparts have palpi that are elongate or flexible, fig. 291,2..**Polyphaga**

Head with only a single median gular suture, no gular sclerite present; anterior portion of head usually prolonged into a beak or snout at end of which are situated the mouthparts, fig. 292*N, O, P*; the latter always having palpi whose segments are fused and immovable........................**Rhynchophora**

Key to Common Families

1. Front of head produced into a definite beak, fig. 319, that may be long or short, the antennae arising from side of beak; palpi vestigial. **Curculionidae,** p. 361

Front of head not produced into a beak; if slightly so, antennae arising between the eyes, or maxillary palpi prominent, fig. 291....................2

2. Middle and hind legs very wide and flat, almost paper-thin, fitted for swimming, the basitarsus large and triangular, the next two produced laterally to form long swimming "fingers"; front legs tubular, fitted for grasping, fig. 292*L;* each eye completely divided, one part on dorsum of head, the other on ventral aspect of head, fig. 292*K*....................**Gyrinidae,** p. 344

Middle and hind legs having some or most segments robust and not flattened, occasionally furnished with rows of long hairs and fitted for swimming in this fashion; eye seldom divided, and then only by a continuation of a head flange or by an antennal base, fig. 294*K*..............................3

3. Maxillary palpi longer than antennae and slender, resembling antennae, fig. 292*Q;* chiefly aquatic...................................**Hydrophilidae**

Maxillary palpi shorter than antennae, and not antenna-like; antennae various 4

4. Antenna with each of last 3 to 7 segments enlarged on one side to form an eccentric plate or lamella, fig. 292*A, C,* each lamella situated nearly at a right angle to long axis of antenna.................................5

Antenna not lamellate, but frequently having the end segments fairly evenly enlarged to form a club, fig. 292*E*, or most of the segments with anterior projections giving a saw tooth, fig. 292*G, J,* or pectinate outline...........6

5. Elytra short and squarely truncate, exposing three full tergites of abdomen, these tergites heavily sclerotized and hard, fig. 295*B*............**Silphidae**

Elytra longer, usually rounded at apex, usually covering entire dorsum of abdomen but in a few species exposing one or two tergites, fig. 311

Scarabeidae, p. 356

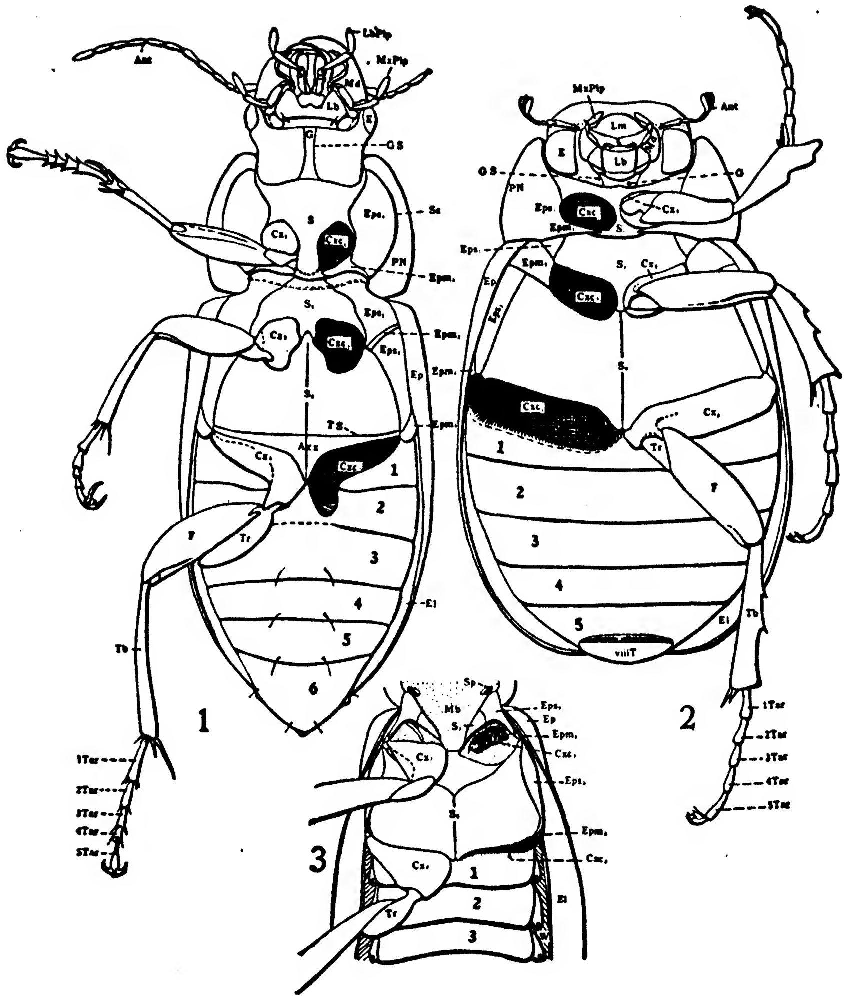


FIG. 291. (1) Ventral view of a ground beetle *Harpalus* sp., Carabidae. Left legs are removed. (2) Ventral view of a May beetle *Phyllophaga* sp., Scarabaeidae. Right legs are removed. (3) Ventral view of part of thorax and abdomen of a soldier beetle *Chauliognathus pennsylvanicus*, Cantharidae. *Acx*, antecoxal piece; *Ant*, antenna; Cx_{1-3}, 1st, 2d, and 3d coxae; Cxc_{1-3}, 1st, 2d, and 3d coxal cavities; *E*, eye; *El*, elytron; *Ep*, epipleuron; Epm_{1-3}, epimera of the pro-, meso-, and metathorax; Eps_{1-3}, episterna of pro-, meso-, and metathorax; *F*, femur; *G*, gula; *GS*, gular suture; *Lb*, labium; *LbPlp*, labial palpus; *Lm*, labrum; *Mb*, membrane; *Md*, mandible; *MxPlp*, maxillary palpus; *PN*, pronotum; S_1, S_2, S_3 pro-, meso-, and metasterna; *Sc*, suture separating pronotum from episternum; *Sp*, spiracle; 1 *Tar* to 5 *Tar*, the five tarsal segments; *Tb*, tibia; *Tr*, trochanter; *TS*, transverse suture; 1 to 6, abdominal sternites; viii*T*, 8th tergite. (After Matheson, "Entomology for Introductory Courses," by permission of Comstock Publishing Co.)

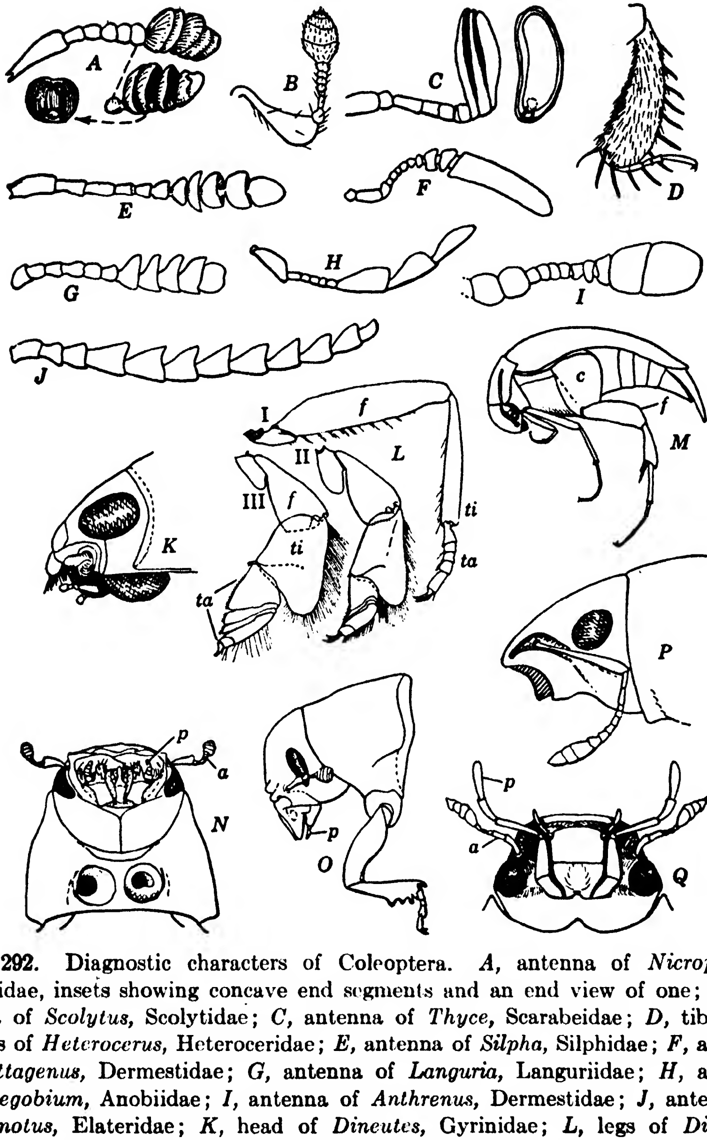


FIG. 292. Diagnostic characters of Coleoptera. *A*, antenna of *Nicrophorus*, Silphidae, insets showing concave end segments and an end view of one; *B*, antenna of *Scolytus*, Scolytidae; *C*, antenna of *Thyce*, Scarabeidae; *D*, tibia and tarsus of *Heterocerus*, Heteroceridae; *E*, antenna of *Silpha*, Silphidae; *F*, antenna of *Attagenus*, Dermestidae; *G*, antenna of *Languria*, Languriidae; *H*, antenna of *Stegobium*, Anobiidae; *I*, antenna of *Anthrenus*, Dermestidae; *J*, antenna of *Melanotus*, Elateridae; *K*, head of *Dineutes*, Gyrinidae; *L*, legs of *Dineutes*, Gyrinidae; *M*, profile of *Mordellistena*, Mordellidae; *N* and *O*, head and prothorax of *Dendroctonus*, Scolytidae; *P*, head of a short-snouted weevil, *Curculionidae; Q*, head of *Tropisternus*, Hydrophilidae. *a*, antenna; *c*, coxal plate; *f*, femur; *p*, maxillary palpus; *ta*, tarsus, *ti*, tibia.

6. Elytra short, exposing five or more sclerotized abdominal tergites, fig. 297*A*..7
Elytra covering all or most of abdomen, never more than two or three sclerotized tergites visible from above; occasionally the abdomen of a female of this group may be extremely distended with eggs, and a third or fourth segment may project from beneath the elytra, but all except the apical two are soft and semimembranous....................................8

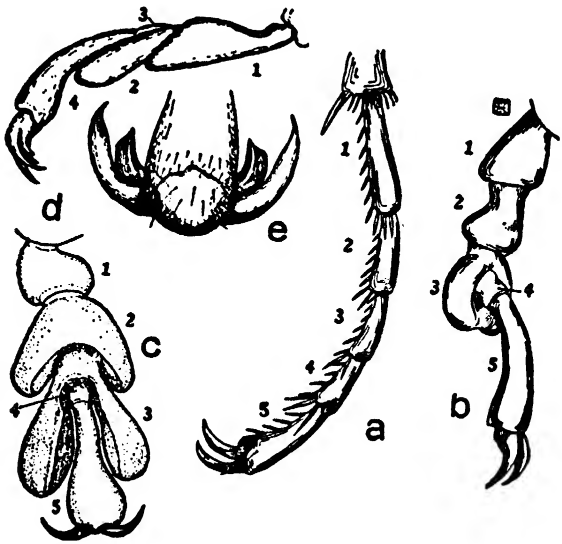


Fig. 293. Tarsi of Coleoptera. *a, Harpalus,* Carabidae; *b, Leptinotarsa,* Chrysomelidae; *c, Chelymorpha,* Chrysomelidae; *d, Epilachna,* Coccinellidae; *e,* toothed tarsal claws. (From Matheson, "Entomology for Introductory Courses," by permission of the Comstock Publishing Co.)

7. Elytra truncate, parallel-sided, and abutting evenly down the meson, fig. 297; abdomen hard and regular in outline................**Staphylinidae,** p. 345
Elytra ovate, fig. 306, overlapping considerably at base; abdomen flabby and shrinking irregularly when the specimen dries............**Meloidae,** p. 352
8. Hind tarsus 4-segmented, front and usually middle tarsi 5-segmented........9
Either hind tarsus having 3 or 5 segments, or all tarsi having the same number of segments..11
9. Body narrow and deep, bilaterally compressed, and with the hind coxa forming a large plate that appears as a major sclerite in the side of the thorax, fig. 292*M*; small beetles often found abundantly in flowers.......**Mordellidae**
Body wider than deep, often flattened, hind coxae no larger than in fig. 291,2 10
10. Each front coxal cavity closed posteriorly by a projection of the pleuron which meets the apex of the sternum, fig. 294*D*; lateral edge of pronotum forming a sharp flange or delineated by a ridge or carina (compare fig. 294*H*)
Tenebrionidae, p. 355

Front coxal cavities open posteriorly, the posteromesal corner of propleuron not extending mesad of outer portion of coxa, fig. 294*C*; lateral edge of pronotum rounding inconspicuously into pleural region.....**Meloidae,** p. 352

11. Head not retracted within prothorax.....12

Head retracted within prothorax, so that only anterior portion protrudes, fig. 294*H*.....14

12. Ventral portion of head having a large convex gular region with a single gular suture down the middle; and the palpi very short or indistinct, fig. 292*N*; antennae always elbowed, with a long first segment, and sometimes ending in a flat club, fig. 292*B*.....13

Ventral portion of head having either a small gular area or two gular sutures, and the maxillary palpi usually much longer, fig. 291,1; antennae not elbowed or the first segment shorter in proportion to the remainder.....14

13. Antenna long, fig. 292*P*, usually ending in a small cylindrical club; side of head having a deep groove for reception of antenna.....**Curculionidae,** p. 361

Antenna short, fig. 292*N*, *O*, ending in a large flat club or comb, fig. 292*B*; side of head without antennal groove.....**Scolytidae,** p. 363

14. Hind and middle tarsi either 3- or 4-segmented, or fourth segment very small in comparison with the third, fig. 293*b*, *c*.....15

Hind and middle tarsi 5-segmented, the fourth as large as or as thick as the third, fig. 293*a*.....27

15. All tarsi having the third segment enlarged, fig. 293*b*, *c*, deeply bilobed or channeled dorsally; the fourth segment extremely small, either sunken into the cleft of the third or arising from dorsum of the base of the third, fig. 293*b*; fifth segment large and normal; frequently the fourth segment cannot be seen, or it appears as a minute subdivision of the base of the fifth segment, in which case each tarsus appears 4-segmented.....16

Either tarsi only 3-segmented, or third segment not enlarged, channeled, or bilobed.....42

16. Antennae longer than the body, fig. 317.....Many **Cerambycidae,** p. 359

Antennae no longer than body.....17

17. Last tergite (pygidium) exposed, almost completely visible beyond or below end of elytra, fig. 294*E*, *F*.....18

Last tergite almost entirely or completely covered by elytra.....21

18. Hind tibia little, if any, longer than basitarsus, and having a pair of long apical spurs, fig. 294*P*.....**Bruchidae,** p. 360

Hind tibia much longer than basitarsus, frequently with only short spurs or none.....19

19. Elytra short, each only about twice as long as wide; stocky short species, the pygidium oblique, and at a definite angle to dorsal contour of the body, fig. 294*F*.....20

Elytra long, each four times or more as long as wide; elongate species, the pygidium nearly horizontal, following dorsal contour of the body, fig. 294*E* some **Cerambycidae,** p. 359

20. Anterior part of prothorax forming a cylinder against which the flat head fits like a lid; eyes oval, fitting against margin of prothorax, fig. 294*H* some **Chrysomelidae,** p. 357

Anterior part of prothorax narrow, head projecting freely beyond it; eyes incised and V-shaped, head constricted behind them, fig. 294*I* most **Bruchidae,** p. 360

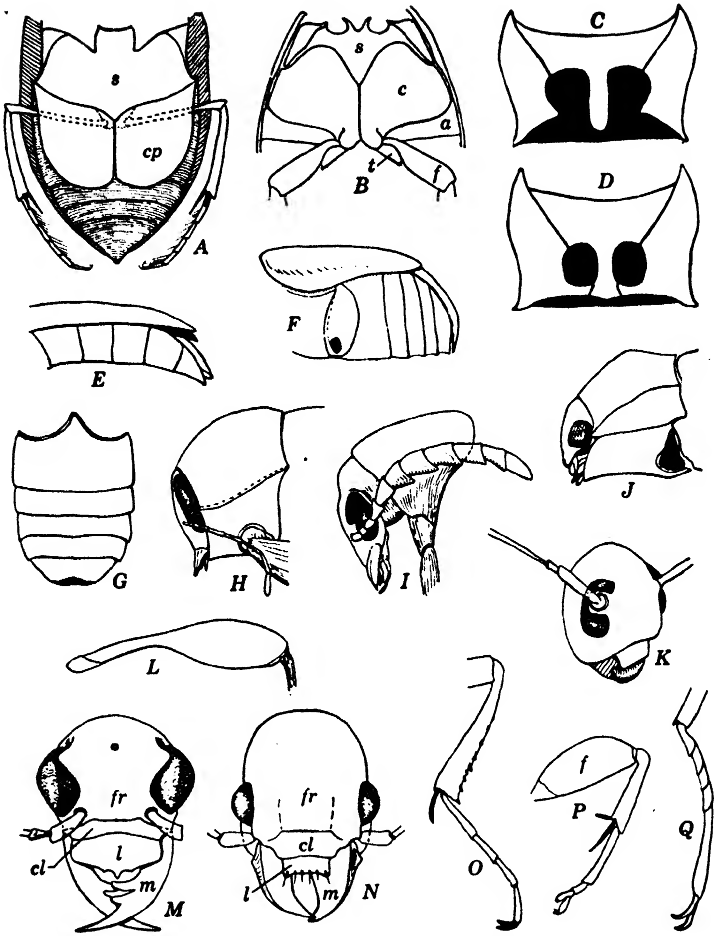


Fig. 294. Diagnostic characters of Coleoptera. *A*, venter of *Haliplus*, Haliplidae; *B*, venter of *Dytiscus*, Dytiscidae; *C*, prosternum showing open coxal cavities, diagrammatic; *D*, prosternum showing closed coxal cavities, diagrammatic; *E*, abdomen of *Leptura*, Cerambycidae; *F*, abdomen of *Bruchus*, Bruchidae; *G*, venter of *Criocerus*, Chrysomelidae; *H*, head and prothorax of *Cryptocephalus*, Chrysomelidae; *I*, head and prothorax of *Acanthoscelides*, Bruchidae; *J*, head and prothorax of *Helichus*, Dryopidae; *K*, head of *Saperda*, Cerambycidae; *L*, hind femur of *Neoclytus*, Cerambycidae; *M*, head of *Cicindela*, Cicindelidae; *N*, head of a Carabidae; *O*, hind leg of *Amphicerus*, Bostrichidae; *P*, hind leg of *Amblycerus*, Bruchidae; *Q*, hind tarsus of *Psephenus*, Psephenidae. *a*, abdomen; *c*, coxa; *cl*, clypeus; *cp*, coxal process; *f*, femur; *fr*, frons; *l*, labrum; *m*, mandible; *t*, *trochanter*.

21. Last 3 to 5 antennal segments enlarged to form a large loose club, fig. 292*G*; elongate, smooth, and highly polished species..................**Languriidae**

Antenna of uniform thickness throughout, or widening gradually to form a club, or forming a round compact club; form various...................22

22. Hind femur greatly enlarged, short, and oval in outline, fig. 316; flea beetles and their relatives...............................**Chrysomelidae,** p. 357

Hind femur elongate or more parallel-sided, or constricted at base and enlarged only at apex, fig. 294*L*...23

23. First abdominal sternite very long, its mesal length nearly equal to that of the following four sternites combined, fig. 294*G*; several genera of varied form (e.g., **Donacia, Crioceris**)....................**Chrysomelidae,** p. 357

First abdominal sternite considerably shorter in proportion to following segments 24

24. Either antenna as long as or longer than body, or hind femur having basal portion slender and apical portion enlarged and clavate, fig. 294*L*
Cerambycidae, p. 359

Antenna shorter than body, and hind femur without a basal stalklike portion 25

25. Tibia having a pair of well-developed tibial spurs at apex
Cerambycidae, p. 359

Tibia having either no tibial spurs or very minute ones..................26

26. Mesal margin of eye deeply incised, with the antenna situated in the incision, fig. 294*K*, or the eye completely divided, the antenna situated between the two parts......................................**Cerambycidae,** p. 359

Either eye not incised, or antenna not at all in incision of eye
Chrysomelidae, p. 357

27. Hind coxa having a wide long ventral plate which covers coxa, trochanter, and most of the femur, fig. 294*A*; small to medium-sized stout aquatic beetles
Haliplidae

Hind coxa at most having only a small outer plate, which does not cover trochanter or femur...28

28. Apices of hind coxae forming a double-knobbed process; base of each coxa extremely large and platelike, appearing as a dominant sclerite of the sternum, fig. 294*B*; hind legs fringed for swimming.............**Dytiscidae**

Hind coxa neither with such a knobbed apex nor with such a platelike base, fig. 291,1,2...29

29. First abdominal sternite completely divided by the hind coxal cavities, the sternite appearing as a pair of triangular sclerites, one on each side of the coxae; first three abdominal sternites immovably united, the separating sutures appearing partly as extremely fine lines, fig. 291,1................30

Either first abdominal sternite not completely or not at all cut into by the coxal cavities, or the first three sternites with separating sutures extremely well developed across the entire width of the segment, as are those between the more apical segments, fig. 291,2...................................31

30. Clypeus fairly narrow, the antennal sockets wider apart than the width of the clypeus, fig. 294*N*..................................**Carabidae,** p. 343

Clypeus much wider, fig. 294*M*, the antennal sockets situated closer together than the width of the clypeus...........................**Cicindelidae**

31. Abdomen having 6 or more exposed sternites 32
Abdomen having not more than 5 exposed sternites, fig. 291,2 35
32. Last 3 to 5 antennal segments enlarged to form a club, fig. 292*E* ..... **Silphidae**
Antenna the same width throughout, often beadlike or serrate 33
33. Tarsus slender and smooth, segments 1 to 4 very short and ringlike, segment 5 long, about equal in length to first 4 combined, fig. 294*Q*; aquatic forms **Psephenidae**
Tarsus stout and densely setose, segment 5 no longer than segment 1, some of the basal segments elongate, as in fig. 293*a* 34

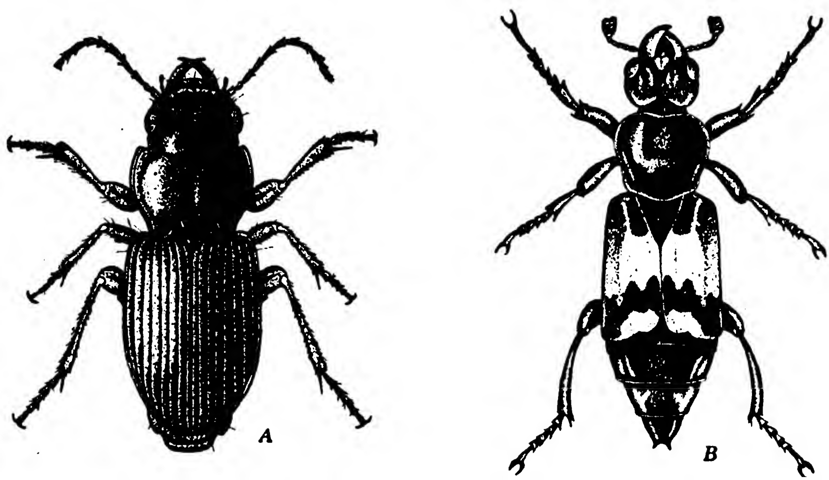


Fig. 295. Beetles. *A,* ground beetle *Pterostichus substriatus; B,* carrion beetle *Nicrophorus marginatus.* (From Kansas State College)

34. Prothorax with broad anterior and lateral margins forming a hood that covers most or all the head from above, fig. 298; head partially retracted, viewed from side .... **Lampyridae,** p. 346
Prothorax not having wide margins, head not retracted in pronotum, hanging down or projecting forward freely .... **Cantharidae**
35. Antenna elbowed and capitate, the club appearing as one round segment, sometimes having faint cross sutures; very hard shining black beetles having short stout legs, the tibiae expanded and spurred for digging, much as in fig. 291,2 **Histeridae**
Antenna not elbowed, and either not thickened toward tip, or the enlarged portion composed of 2 or 3 well-separated segments or a single elongate segment; legs or body shape different to above 36
36. Antennae elongate and serrate throughout, fig. 292*J* 37
Antennae short, filiform, or clavate 38
37. Pronotum having a sharp projection at each posterolateral corner, fig. 299 **Elateridae,** p. 347
Pronotum having posterolateral corners rounded and not pointed, fig. 301 **Buprestidae,** p. 348

38. Prosternum produced anteriorly to form a long concave shelf under the head, the latter largely retracted into the opening of the prothorax, fig. 294*J*....39
Prosternum not so produced, much shorter than pronotum and proportioned more as in fig. 294*I*; head usually held downward against chest............40
39. Front coxae round, situated some distance from lateral edge of pronotum; antennae elongate or definitely clavate..........................**Elmidae**
Base of front coxae triangular, the point of the triangle extending nearly to lateral edge of prosternum, fig. 294*J*; antennae short, the flagellum of equal thickness throughout, with wide flat segments............**Dryopidae,** p. 348
40. Antennae ending in a distinct club composed of 1 to 3 segments, fig. 292*F,I* **Dermestidae,** p. 349
Last 3 segments of antenna greatly enlarged but well separated to form a chain, fig. 292*H*...41
41. Tibiae without spurs; small convex forms including drugstore and cigarette beetles, infesting dried food products..........................**Anobiidae**
Tibiae with distinct spurs, fig. 294*O*; includes many subcylindrical forms ornamented with horny processes and ridged areas; the powder post beetles **Bostrichidae**
42. Front and middle tarsi 4-segmented, hind tarsus 3-segmented......**Cucujidae**
All tarsi having the same number of segments..........................43
43. Tarsi 4-segmented, all segments well marked, and second and third of about equal width..44
Tarsi 3-segmented, or third segment minute and hidden at the base of an enlarged second segment, fig. 293*d*..................................45
44. Tibiae dilated and armed with a series of stout spurs, fitted for digging, fig. 292*D*; molelike beetles covered with dense pile, inhabiting wet mud or sand banks..**Heteroceridae**
Tibiae either not dilated or not armed with a series of spurs; flat beetles found under bark or in stored grain and feed...................**Cucujidae**
45. Second segment of tarsus dilated, with a large ventral pad, fig. 293*d*; almost hemispherical beetles, usually polished and strikingly patterned **Coccinellidae,** p. 349
Second segment of tarsus not much if at all wider than first segment; beetles often somewhat angular in outline, and flat; frequenting flowers, and tree sap..**Nitidulidae**

Suborder ADEPHAGA

This suborder contains eight families, most of them predaceous, feeding on other insects. Four families are terrestrial and four aquatic; of the latter, both adults and larvae live in the water. Two families of the Adephaga are extremely abundant: the Carabidae and Gyrinidae.

Carabidae, Ground Beetles. These are active terrestrial species with long slender antennae of even thickness, long elytra, and long legs suitable for running, fig. 295*A*. They vary in size from 1 mm. in length to large metallic-colored species 35 mm. long. The mouthparts are well developed, and the mandibles are long, strong, and sharp. The adults are almost entirely nocturnal, hiding during the day in logs or cavities and under ground cover or stones. They come out at night to forage for prey. A wide variety of animals, including snails, worms, and adult and immature insects of many kinds, makes up their food. The larvae are slender, with strong mouthparts, well-developed legs, and a pair of terminal *urogomphi* (cercus-like organs). They are predaceous, feeding on other insects. They are usually found in the soil or under ground cover, where they hunt their prey. The family is a large one, embracing over two thousand nearctic species.

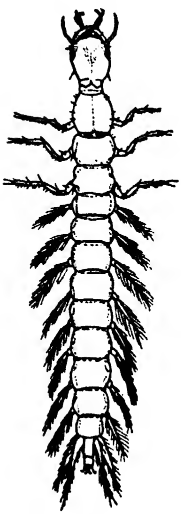


FIG. 296. Larva of whirligig beetle. (Redrawn from Böving and Craighead)

Gyrinidae, Whirligig Beetles. Aquatic beetles, the adults hard, convex, shining, and dark. The middle and hind legs are broad, fringed with hair, and used for swimming. The head has two peculiarities: (1) short antennae with an earlike expansion of the third segment, and (2) eyes that are completely divided into an upper and a lower half, so that the beetle appears to have two pairs of eyes, fig. 292*K*. The adults are common in lakes and streams. They congregate in swarms of thousands, and zigzag along the surface, moving at high speed and leaving silvery crisscrossing wakes which are a familiar sight to every naturalist. During these surface gyrations, the divided eyes give the beetles the opportunity of seeing into the air with the dorsal eyes and into the water with the ventral pair. The larvae, fig. 296, are slender, white-bodied, and elongate. Each segment of the abdomen has a pair of long tracheal gills, and at the end of the abdomen are a pair of hooks. Both adults and larvae are predaceous, the adults feeding chiefly on small organisms falling or alighting on the water surface, the larvae on small organisms they find in sheltered places on the bottom of the pond or stream.

Suborder POLYPHAGA

This includes the great bulk of the beetles, containing over one hundred and thirty families, and embracing forms diverse in appearance and life history. Some families, such as the Chrysomelidae and Coccinellidae, are abundant and include species of considerable economic importance. Many families, however, are rare or seldom seen except as a result of specialized collecting and have no known economic importance. There are certain groups of families which form fairly definite units of closely related forms, and families from a selection of these are discussed in the following paragraphs.

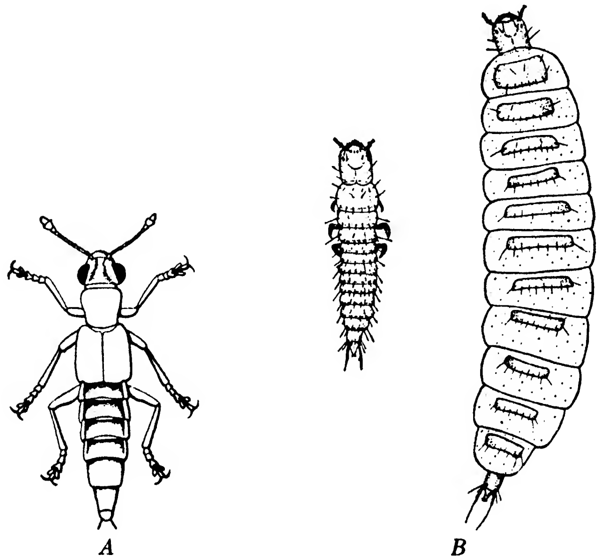


FIG. 297. Rove beetles. *A, Stenus* adult; *B,* first-instar larva of *Aleochara curtula,* left, before feeding; right, full grown. (*A,* after Sanderson; *B,* modified from Kemner)

Staphylinidae, Rove Beetles. Slender elongate beetles, fig. 297*A*, with short truncate elytra beneath which the pair of flying wings are folded. The antennae are fairly long, either filiform or slightly enlarged at the tip. The larvae are also elongate and look much like small carabid larvae. Both adults and larvae are scavengers or predators, with the exception of a few species that have parasitic larvae. The adult rove beetles are found on flowers, in ground cover, under bark, in rotting organic material, in ant and termite nests, and in many other situations. The larvae are more secretive and occur chiefly in humid places. The species that are predaceous feed on mites, small insects, insect and mite eggs, and especially on small dipterous larvae. Certain species are valuable factors in the natural control of pests. An interesting example is the genus *Baryodma,* whose larva is a parasite of the cabbage-maggot pupa. The larva of *Baryodma* is unusual in that during the first instar it is a slender free-running form with relatively large tergal plates. It searches in the soil for a fly puparium and enters it by boring an opening. In the puparium the beetle larva feeds on the fly pupa and grows amazingly, becoming greatly distended and grublike before molting. Later instars are always grublike. The same phenomenon occurs in some species of *Aleochara,* fig. 297*B*.

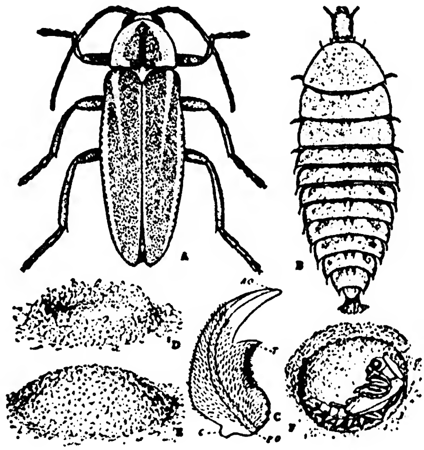


FIG. 298. A firefly *Photurus pennsylvanicus*. *A,* adult male; *B,* mature larva; *C,* left mandible of larva to show mandibular canal. *AO,* opening of canal; *PO,* opening of canal to mouth; *C,* condyle; *T,* tooth on mandible; *D,* beginning of pupal chamber; *E,* completed pupal chamber; *F,* pupa in chamber. (From Matheson, after Hess)

Lampyridae, fireflies. These are moderate-sized soft-bodied beetles, having serrate antennae and having the margins of the pronotum projecting like a flange or shelf, which partially covers the head. The elytra are relatively soft. A common eastern species is *Photurus pennsylvanicus,* fig. 298. The adults occur in summer and fly actively on warm nights, almost invariably following a dipping up-and-down course only a few feet above the ground. As they start their "upstroke," each individual flashes a bright light, a mating signal. When swarms of adults are on the wing, the entire countryside is lighted up with these tiny dots of light. From this comes the name firefly. In certain genera the females are wingless and grublike; these and the larvae are also luminous and are called glowworms. Both larvae and adults are predaceous, although some adults may feed partly on plant material or not at all.

Elateridae, Click Beetles or Wireworms. The adults are trim and hard bodied, fig. 299*a*, having five-segmented tarsi, a large pronotum with sharp posterior corners, serrate antennae, and a long stout sharp process projecting backwards from the prosternum. If placed on

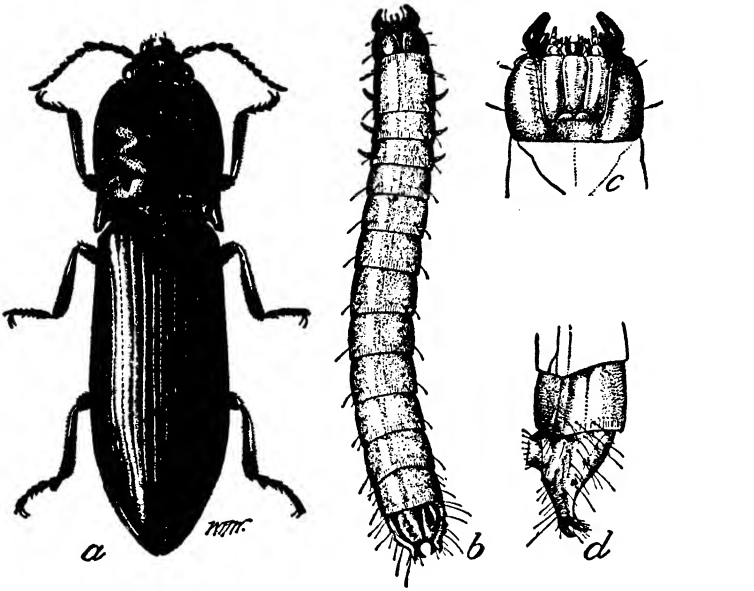


Fig. 299. The dry land wireworm *Ludius inflatus*. *a*, adult; *b*, larva; *c*, ventral aspect of larval head; *d*, lateral aspect of larval abdomen. (From U.S.D.A., B.E.P.Q.)

their backs, these beetles can spring several inches into the air, at the same time making a loud click, usually alighting right side up. This leap is engineered by using the ventral process of the prosternum as a sort of spring release when the body is tensed. The adults are frequently encountered during spring and summer. These beetles and their acrobatics are well known to youngsters in rural districts.

The larvae, called wireworms, fig. 299*b*, are wormlike and hard-bodied and live in soil or rotten wood. The soil-inhabiting larvae feed on roots of grasses and related plants and are extremely destructive to many of the grain crops. Especially injurious are species of the genera *Melanotus*, *Agriotes*, and *Monocrepidius*. Several hundred species occur in North America. Of unusual interest to the collector immature insects are the odd wormlike larvae of the group to which *Horistonotus* belongs, fig. 300.

Buprestidae, Metallic or Flatheaded Wood Borers. These beetles, fig. 301, resemble the click beetles in that the adults have serrate antennae, five-segmented tarsi, and hard bodies, but they differ in having the first two sternites of the abdomen fused and in the coppery or bright metallic coloring of the body and elytra. They are usually more robust and have a shorter pronotum. The larvae, fig. 301, of the larger species bore in wood, attacking live trees or newly felled or killed trees, and feeding either beneath the bark or into the solid wood. These larvae are legless and elongate, having the thorax expanded and flattened. They attack a wide variety of trees, including deciduous and coniferous species. The flatheaded apple tree borer *Chrysobothris femorata* is often an orchard pest of importance. A few genera of small buprestids have leaf-mining larvae, which are more cylindrical than the wood borers and have minute legs.

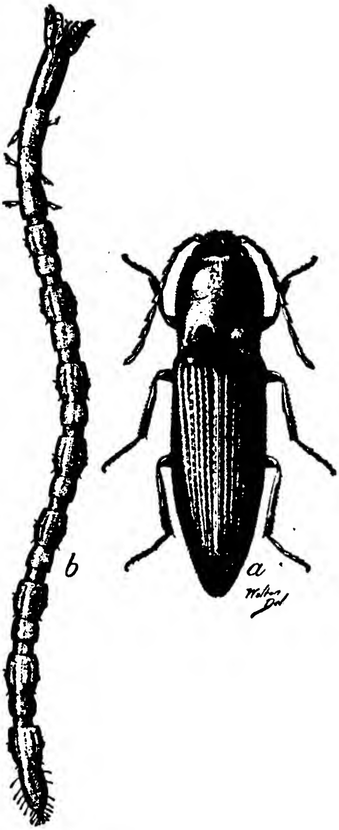


Fig. 300. The sand wireworm *Horistonotus uhlerii.* *a*, adult; *b*, larva. (From U.S.D.A., B.E.P.Q.)

Dryopidae and Their Allies, the Dryopid Beetles. In this group of aquatic beetles both the adults and larvae live in the water. Both are sluggish, crawling over stones or submerged wood, and feeding on surface encrustments. The adult is clothed with fine hair which holds a film of air when under water. The insect uses this film as a means of gas exchange with the surrounding water. The larvae respire by means of tracheal gills situated on various parts of the body, many retractile within ventral pouches. As with other aquatic Coleoptera, the mature larvae leave the water and pupate in damp soil. Most of the dryopids live in cold rapid streams and are frequently found in large numbers in siftings from gravel bars. The adults leave the water periodically for mating or dispersal flights.

Dermestidae, Carpet Beetles. Convex oval beetles, having short clubbed antennae, five-segmented tarsi, and abdomens with only five sclerotized sternites, fig. 302*a*. The larvae are elongate or oval, clothed distinctively with large tufts or bands of long barbed hair, figs. 302*B*, 303*A*. They feed on dried animal products, including fur,

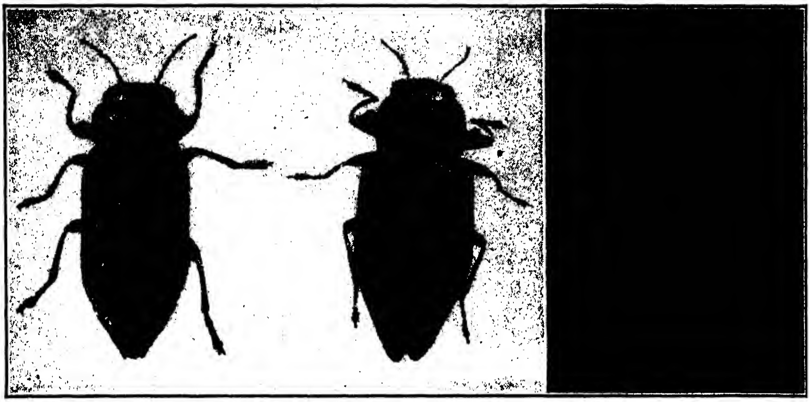
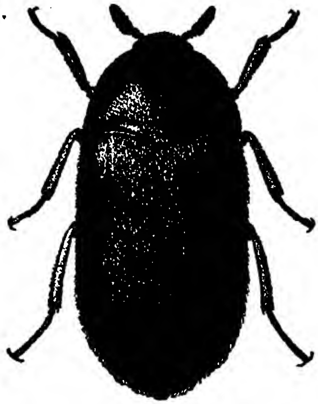


FIG. 301. Buprestidae. Left, the flatheaded appletree borer, *Chrysobothris femorata;* center, the Pacific flatheaded borer, *C. mali;* and, right, larva in burrow. (From U.S.D.A., B.E.P.Q.)

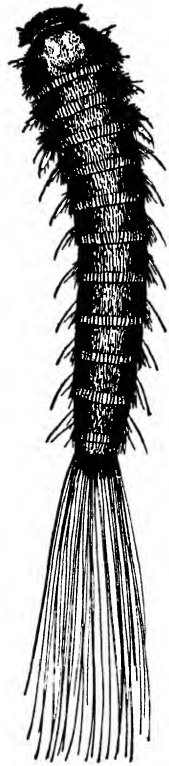
skins, and dried meat. The last is attacked readily by species of the genus *Dermestes*, especially *D. lardarius* the larder beetle. Some of the smaller species, particularly the carpet beetle *Anthrenus scrophulariae*, fig. 303, and the black carpet beetle *Attagenus piceus*, fig. 302, attack furs, carpets, and upholstery, in fact, anything made from animal hair. These pests are so widespread that they are a constant menace to household goods and many stored materials. In nature the species feed on dead insects or animal carcasses. The adults feed on the same material as the larvae, but during dispersal flights they feed on pollen and at this time are often found on garden flowers.

Coccinellidae, Ladybird Beetles. Moderately small round convex shining beetles, fig. 304, sometimes prettily patterned with red, yellow, black, or blue markings. The antennae are short and clavate. The tarsi are four-segmented but appear to be three-segmented; the third segment is extremely minute, situated between the padlike second segment and the large end segment bearing the claws. The

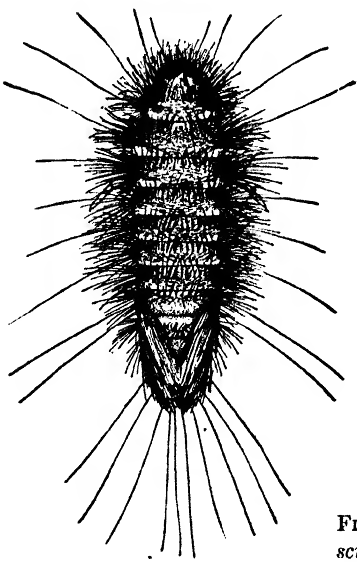


A

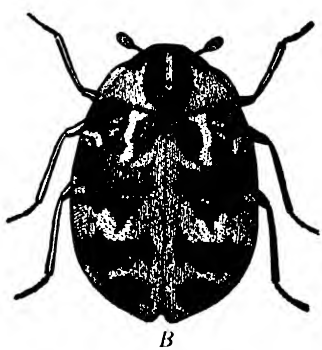
Fig. 302. The black carpet beetle *Attagenus piceus*. *A*, adult; *B*, larva. (From Connecticut Agricultural Experiment Station)



B



A



B

Fig. 303. The buffalo carpet beetle *Anthrenus scrophulariae*. *A*, larva; *B*, adult. (From Connecticut Agricultural Experiment Station)

larvae either are warty creatures or are covered with a waxy secretion and have extremely short antennae but long legs. Two categories of ladybird beetles are of economic importance. Species of the first feed on aphids and scale insects and function as effective means of natural control against some of these pests. The best known of these

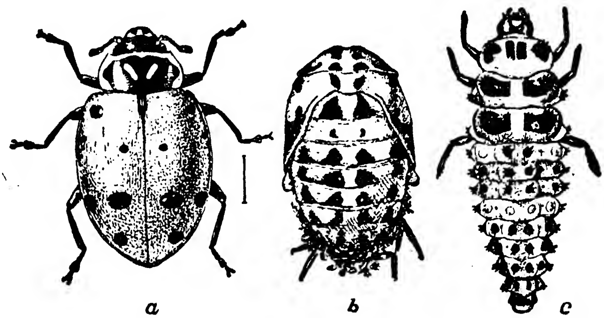


FIG. 304. A ladybird beetle *Hippodamia convergens*. *a*, adult; *b*, pupa; *c*, larva. (From U.S.D.A., B.E.P.Q.)

predators is the vedalia *Rodolia cardinalis*, a native of Australia, which was introduced into California for the control of the cottony-cushion scale. The vedalia has been very effective in this capacity. A common and widespread native species is *Hippodamia convergens*,

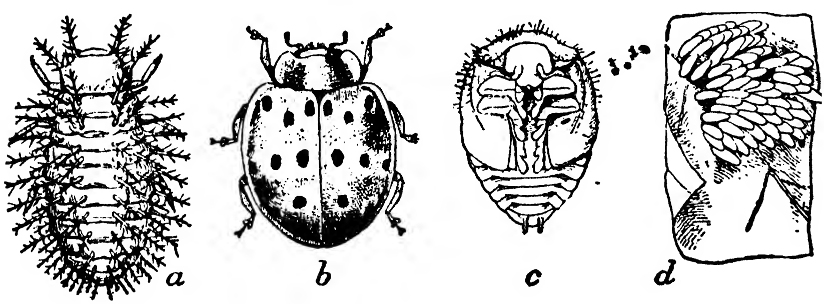


FIG. 305. The Mexican bean beetle *Epilachna varivestis*. *a*, larva; *b*, adult; *c*, pupa; *d*, eggs. (From U.S.D.A., B.E.P.Q.)

fig. 304. The second important category of ladybird beetles includes plant-feeding species. In North America the Mexican bean beetle, *Epilachna varivestis*, fig. 305, is one of the most destructive defoliators of beans in many central and southern areas. Both adults and larvae feed on the foliage.

Meloidae, Blister Beetles. The adults, fig. 306, are moderately large beetles with relatively soft bodies and elytra, long simple antennae, and a prominent round or oval head that is well set off from the thorax. The tarsi of the front and middle legs are five-segmented, but the tarsi of the hind legs are four-segmented. This characteristic marks off a group of some twenty beetle families sometimes referred

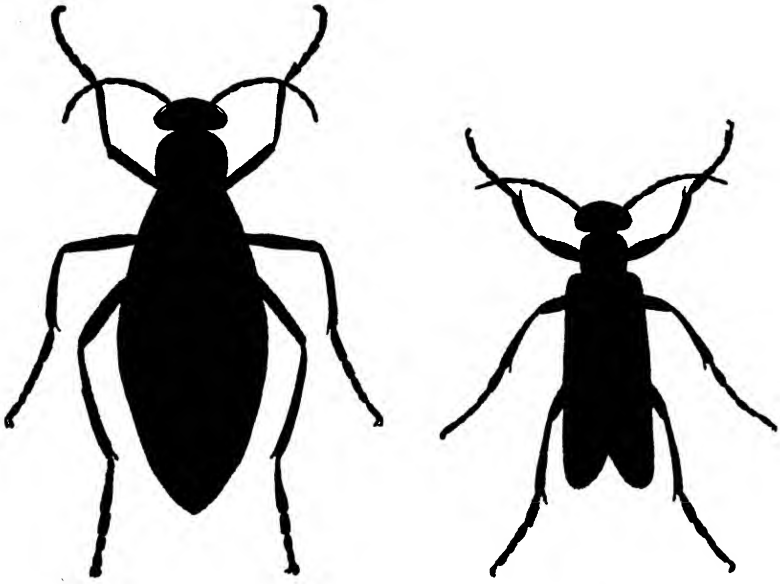


FIG. 306. Adults of blister beetles. *A, Henous confertus; B, Epicauta pennsylvanica.* (After Horsfall)

to as the *Heteromera.* The blister beetles contain an oil, cantharidin, which is a powerful skin irritant and causes the formation of large water blisters on human skin. A sufficient amount of cantharidin to cause irritation is picked up by just handling the live adults.

The life history of the Meloidae, as exemplified by *Epicauta pennsylvanica,* fig. 307, presents several conditions greatly at variance with those found in most of the Coleoptera. Preparatory to oviposition, the female digs a hole about an inch deep in the soil, then at the bottom deposits a mass of fifty to three hundred eggs, and fills up the hole with soil. The eggs hatch in about a week, the resulting larvae being very active, slender, and well sclerotized. These, called triungulins, make their way to the surface and wander about in search of food. The majority of the common species feed on grasshopper

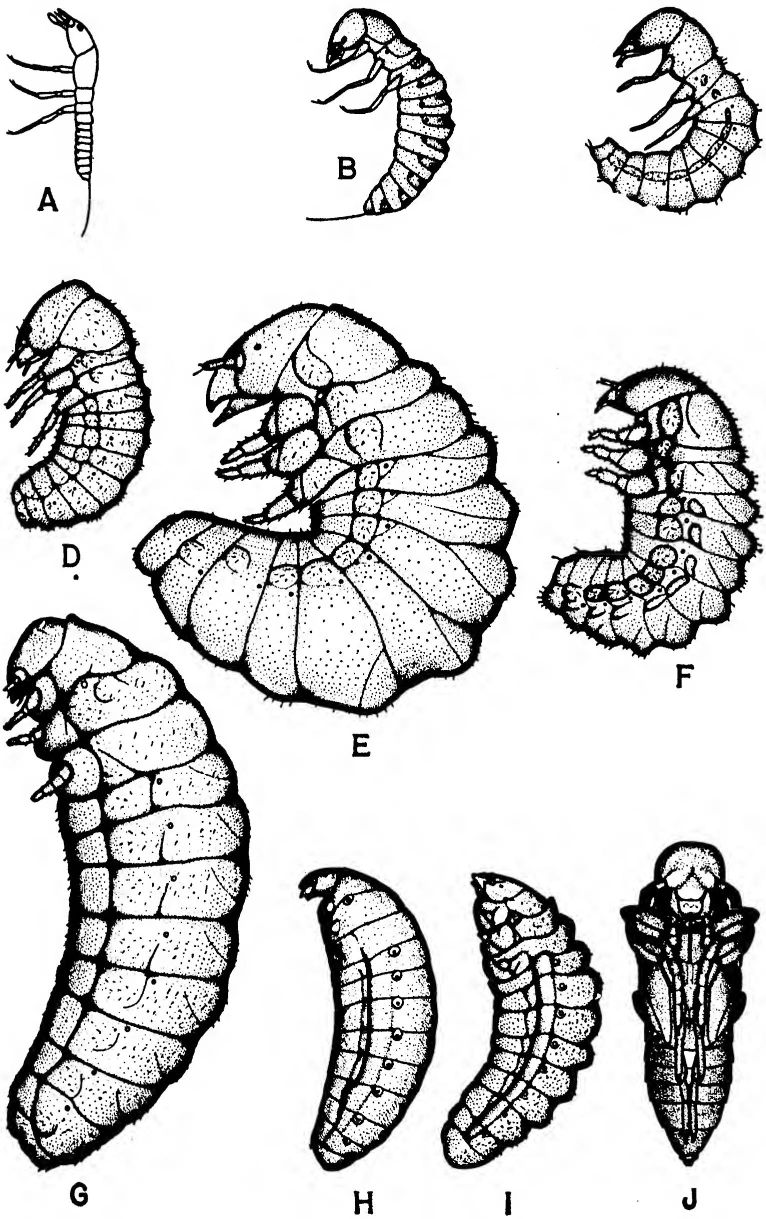


FIG. 307. Immature stages of the black blister beetle *Epicauta pennsylvanica*. *A*, unfed first instar; *B*, fully fed first instar; *C, D, E*, second, third, and fourth instars; *F*, newly molted fifth instar; *G*, gorged fifth instar; *H*, sixth instar; *I*, seventh instar; *J*, pupa. *A–E*, ×17; *F, G*, ×9; *H–J*, ×5. (After Horsfall)

eggs. The triungulin seeks out the grasshopper egg masses, digs down to them, punctures an egg, and starts feeding on its contents. In a few days, when the triungulin is swollen and fully fed, the first molt occurs. The grublike thin-skinned second instar is relatively inactive and continues feeding on the grasshopper egg mass.

The third, fourth and fifth instars follow in rapid succession and are similar to the second. The fifth instar, when full grown, leaves the food mass, burrows a few inches farther into the soil, and makes

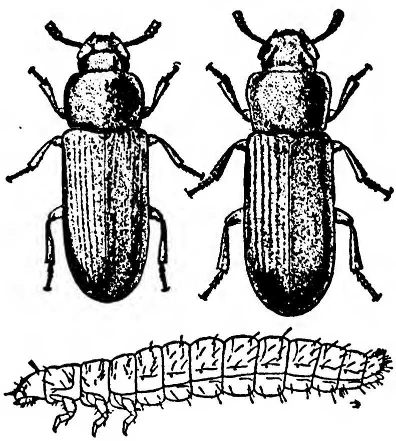
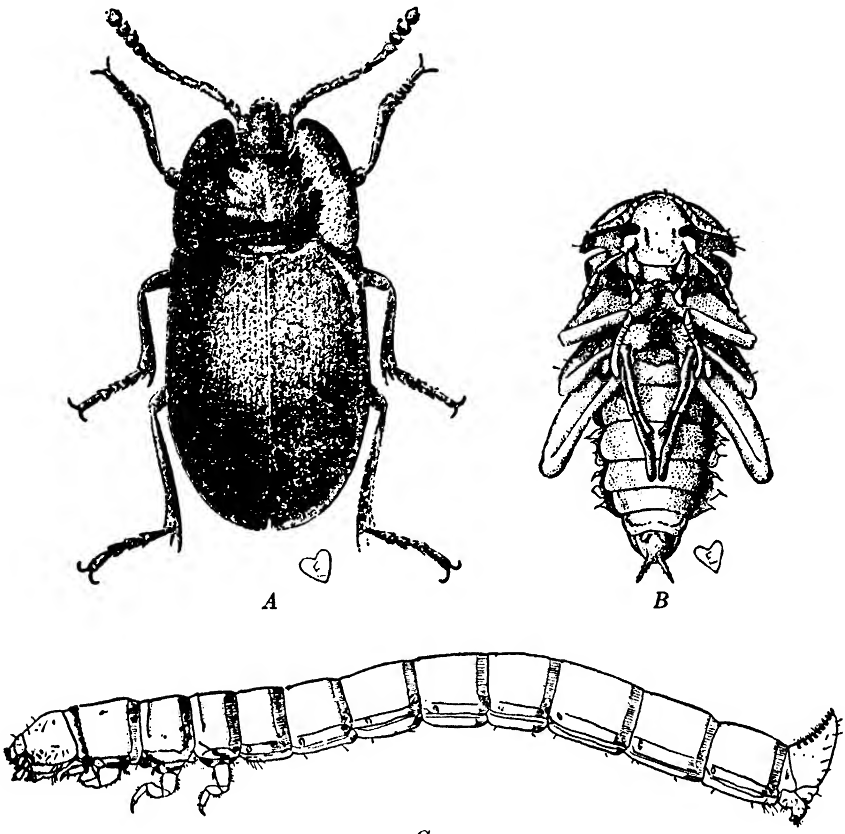


FIG. 308. The rust-red flour beetle *Tribolium castaneum,* and the confused flour beetle *Tribolium confusum.* Below, larva of *T. castaneum.* (From U.S.D.A., B.E.P.Q.)

an earthen cell in which it molts to form the sixth-instar larva. This sixth instar, called the coarctate form, is unique among beetles. It is non-feeding, heavily sclerotized, oval in shape, and rigid. Only humplike legs are present. Usually the winter is passed in this stage. The next summer the coarctate larva molts to form a seventh instar much like the fifth; this larva gives rise to the pupa, which transforms in a few weeks to the adult. The coarctate larva is extremely resistant to desiccation, and it provides a margin of safety to the species in drought years. For, if conditions are too dry during the summer after hibernation, the coarctate larva will not molt, but will "lay over" an additional year or even 2 years, if necessary, when less arid conditions prevail and the normal life cycle can be resumed.

Meloid adults are leaf feeders and cause appreciable damage to potatoes, tomatoes, squash, certain legumes, and other crops. The three-striped blister beetle *Epicauta lemniscata* is a colorful representative often injurious to these plants. One of the species frequently feeding on potatoes, *Meloe angusticollis,* is unusual among beetles in that the elytra overlap at the base. Another short-winged meloid is the squash blister beetle *Henous confertus.*



A B

C

FIG. 309. A false wireworm *Embaphion muricatum.* *A,* adult; *B,* pupa; *C,* larva. (From U.S.D.A., B.E.P.Q.)

Tenebrionidae, the Darkling Beetles. Hard-shelled beetles, normally dark in color, and oval or parallel-sided in outline, fig. 308; tarsi of the front and middle pairs of legs are five-segmented, those of the posterior legs four-segmented; antennae moderately long, usually filiform or clavate. The larvae feed chiefly on dead plant material and fungi, especially bracket types, or mycelium in rotten wood; a few are predaceous, and a few attack stored grain. The larvae are elongate and cylindrical, with stout legs. Those of the western genus *Eleodes* feed on plant roots and are called false wireworms because of their resemblance to true wireworms (Elateridae larvae). Another western false wireworm is *Embaphion muricatum,* fig. 309, whose larva is destructive to wheat. Some of the species attacking stored grains and prepared foods are widespread and cause large commercial loss. Among this group are the mealworms *Tenebrio sp.,* which are relatively large, the adults reaching a length of 15 mm. and the larvae 25 or 30 mm.; and the confused flour beetle *Tribolium confusum,* and several related species of *Tribolium,* which are very small, the adults being only 3 or 4 mm. in length.

Scarabeidae, the Lamellicorn Beetles, or Scarabs. This is one of the largest families of beetles, characterized most conspicuously by the

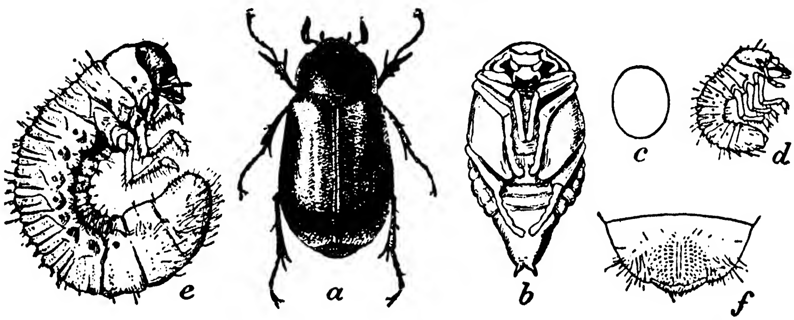


FIG. 310. A May beetle *Phyllophaga arcuata.* *a,* adult; *b,* pupa; *c,* egg; *d,* first-instar larva; *e,* mature larva (white grub); *f,* anal segment of larva, ventral aspect. (From U.S.D.A., B.E.P.Q.)

lamellicorn antennae, in which the apical segments are leaflike and appressed in repose. The scarabs vary greatly in size and shape; most of them are stout and very hard shelled; the larvae are sluggish, stout, usually white, and with a characteristic curved outline, fig. 310; a number of groups of scarabs are scavengers, and feed on dung, rotting hides, or fungi. Of unusual interest are *Canthon* and certain other genera; the adult fashions a ball of dung, rolls it away, and buries it. Eggs are laid on this ball, and the developing larvae utilize it as food. The remainder of the scarabs are phytophagous, many species of great economic importance. The most publicized member of the family is the Japanese beetle *Popillia japonica,* fig. 311; the larvae feed on grass roots and are especially destructive to lawns and golf courses, and the adults defoliate fruit and shade trees.

Another group of destructive species are the June beetles, members of the genus *Phyllophaga;* the adults defoliate deciduous trees, and the larvae, known as white grubs, eat the roots of various grass crops, including corn, small grains, and pasture plants.

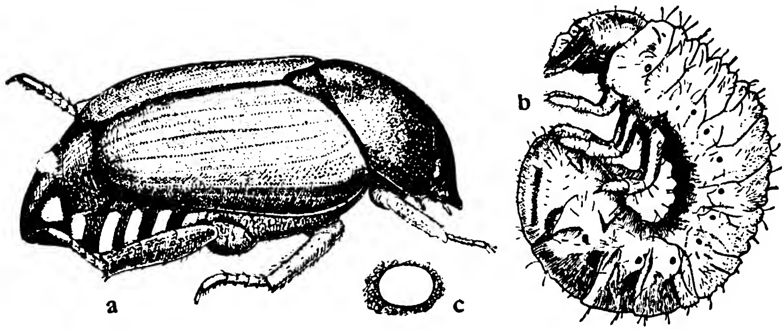


Fig. 311. The Japanese beetle *Popillia japonica.* (From Connecticut Agricultural Experiment Station)

In the tropics there are many species of large scarabs, often brilliantly colored or ornamented with spines or projections on the head or pronotum. In the United States the largest species is *Dynastes tityus* the rhinoceros beetle, which is larger than a mouse, fig. 312. The larva lives in rotten wood.

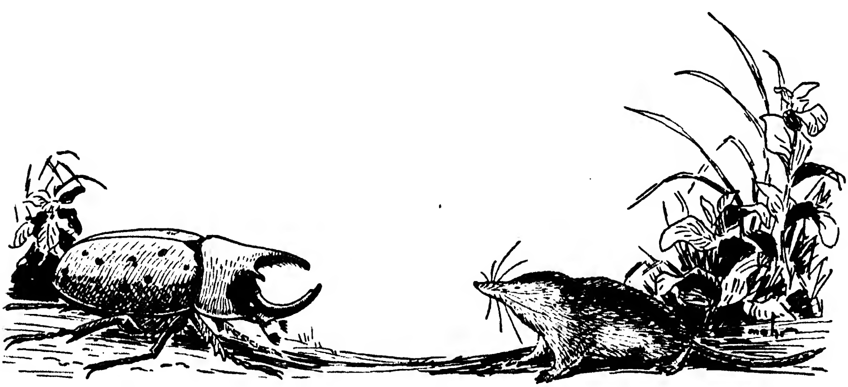


Fig. 312. *Dynastes tityus,* Illinois' largest beetle, and a shrew *Sorex longirostris,* Illinois' smallest mammal. (Drawing loaned by C. O. Mohr)

Chrysomelidae, the Leaf Beetles. These comprise a large family, the species small to moderate in size, usually oval, stout, or wide bodied, and having filiform fairly long antennae, fig. 313. The most outstanding characteristics are found in the tarsi, fig. 293*b*, *c*. These appear four-segmented; the third segment is enlarged to form a large kidney-shaped pad; the last segment, really the fifth, is long and slender and appears to be attached within the median incision of the third; actually the fourth segment is an extremely reduced ring at the base of the fifth, but it is so small that it is seldom seen without one's first mak-

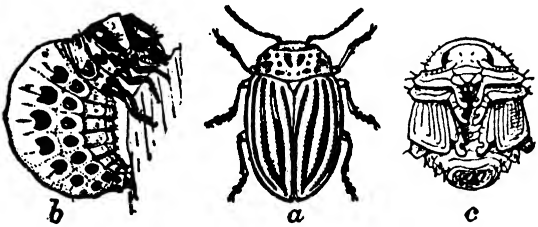


FIG. 313. The Colorado potato beetle *Leptinotarsa decemlineata.* *a,* adult; *b,* larva; *c,* pupa. (From U.S.D.A., B.E.P.Q.)

ing a special preparation of the leg. The larvae of the leaf beetles are varied, but most of them are stout grubs with short legs and antennae; a number bear spines and processes; and some of the leaf mining species are long and flat. The eggs are laid in soil or under bark or deposited on stems or leaves.

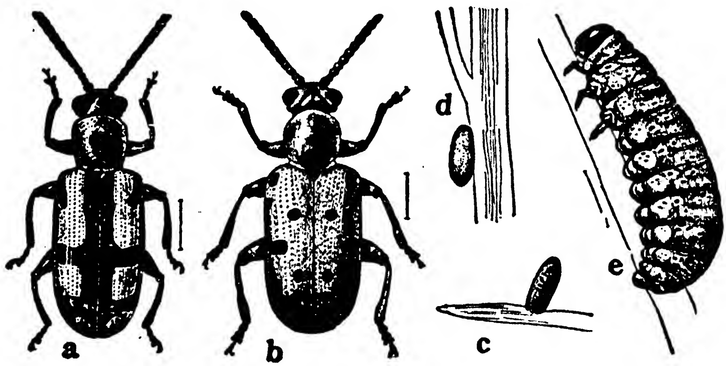


FIG. 314. Asparagus beetles. *a, Criocerus asparagi; b, Criocerus duodecimpunctata; c,* egg of *C. asparagi* on leaf; *d,* egg of *C. duodecimpunctata* placed parallel to stem; *e,* larva of *C. asparagi.* (From U.S.D.A., B.E.P.Q.)

With few exceptions adult Chrysomelidae feed on plant foliage, and their larvae on roots or leaves. Many attack commercial crops, and the family includes a large number of important economic species. The Colorado potato beetle *Leptinotarsa decemlineata,* fig. 313, is one of the most destructive insects attacking potato; both larvae and adults feed on the foliage. The asparagus beetle *Criocerus asparagi,* fig. 314, is a common showy species wherever asparagus is grown; both larvae and adults feed on the foliage; the eggs are black and stuck by one end into the heads of the plants. The larvae of many species, such as *Diabrotica vittata,* fig. 315, are known as rootworms. The adults of many small species jump like fleas and for this reason are called flea beetles. Of these, the genera *Phyllotreta* and *Epitrix* contain several species whose adults eat holes in leaves, and the elongate

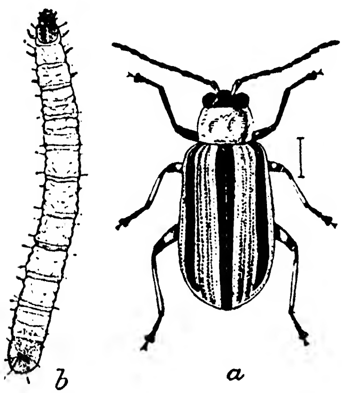


FIG. 315. The striped cucumber beetle *Diabrotica vittata.* *a,* adult; *b,* larva. (From U.S.D.A., B.E.P.Q.)

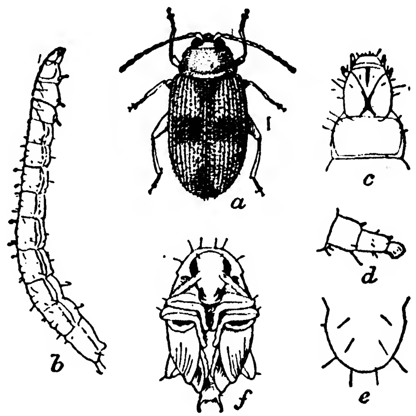


FIG. 316. The tobacco flea beetle *Epitrix hirtipennis.* *a,* adult; *b,* larva; *c,* head of larva; *d,* posterior leg of same; *e,* anal segment, dorsal view; *f,* pupa. (From U.S.D.A., B.E.P.Q.)

larvae eat roots of cabbage, turnips, potatoes, cucumbers, and other plants. An important species is the tobacco flea beetle *Epitrix hirtipennis,* fig. 316. Not all flea beetles have root-feeding larvae; those of the genus *Haltica,* for instance, are leaf feeders like the adults.

Cerambycidae, Longhorn Beetles. Elongate beetles, many of them attractively colored, having long legs and unusually long antennae, fig. 317. In other characters the longhorns are almost identical with the Chrysomelidae, including the curious tarsi with the enlarged third segment and the reduced fourth. The larvae of the longhorns are cylindrical and elongate, with a round head, and either no legs or minute ones; they are known as roundheaded borers. Most of them bore either in the cambium layer or through the heartwood of trees; a few bore in the roots and lower stems of succulent herbs such as milkweeds and ragweeds, or in the stems of shrubs such as willow and raspberries. Certain species are of considerable economic importance.

The roundheaded apple tree borer *Saperda candida*, fig. 317, is a brown and white striped species that is locally a serious pest of apple, the larvae boring through the trunk and making extensive tunnels. The locust borer *Cyllene robiniae* has a handsome adult with a geometric yellow pattern on black; its larvae bore in young black

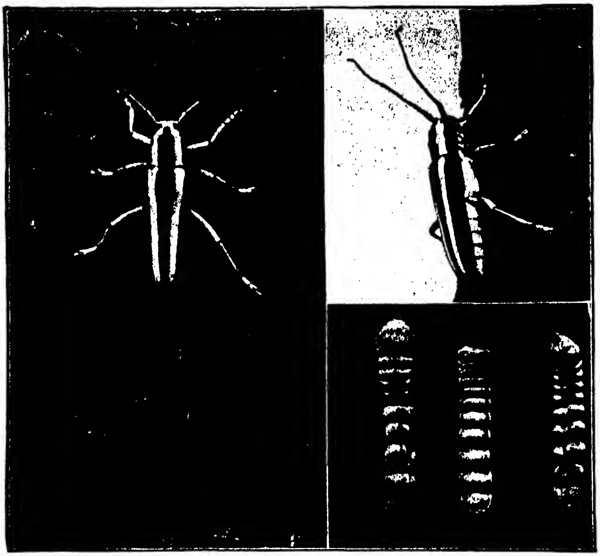


FIG. 317. The apple tree borer *Saperda candida;* larvae, adults, and exit holes, natural size. (After Rumsey and Brooks)

locust trees and weaken them so that wind breaks them easily; many black locust plantings, established for soil-erosion purposes, have been entirely destroyed in this manner.

Most of the longhorn species are pests of forest trees, attacking both deciduous and coniferous species. Under improper or careless lumbering conditions or unusual weather, various longhorn species may become abundant enough to cause considerable loss to commercial stands of trees.

Bruchidae, Bean and Pea Weevils. This is a most interesting family closely related to the Chrysomelidae. The adults are short and stout; the larvae are grublike and almost legless, living inside legume seeds. Several species are pests of considerable importance in various kinds of stored peas and beans; a common example is the pea weevil *Bruchus pisorum,* fig. 318.

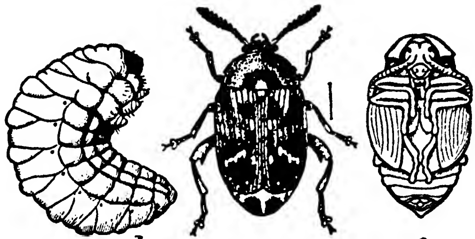


FIG. 318. The pea weevil *Bruchus pisorum.* *a,* adult; *b,* larva; *c,* pupa. (From U.S.D.A., B.E.P.Q.)

Other Polyphaga. The families mentioned are only a few of the many beetle families in the suborder Polyphaga. Concerning families not discussed here, students will find a great deal of information on life history and identification in the books listed at the end of the section on Coleoptera (see p. 367).

Suborder RHYNCOPHORA

The snout beetles or weevils are the most distinctive of the Coleoptera. No other group of beetles has a snout at all like that of the typical weevils. The converse, however, is not true; some members of the Rhyncophora have no pronounced beak, and their diagnosis is on the basis of the sutures of the head and thorax, as outlined in the key on page 335. Several families are included in the suborder, of which the Curculionidae and Scolytidae are of chief importance.

Curculionidae, Typical Weevils. Head with a definite beak, sometimes elongate and curved, fig. 319; antennae usually elbowed and clubbed; body, elytra, and legs very hard, forming a solid well-armored exterior. The larvae are legless grubs, usually having dark head capsules and white bodies.

The Curculionidae is a large family, containing over two thousand nearctic species and many extremely important economic species. The larvae feed on plant material in a variety of ways; they include root feeders, stem borers, leaf feeders, and those which feed in fruits such as hazelnuts, acorns, cherries, and plums; in rotten wood; or in stored grain. The adults usually feed on the leaves or fruiting bodies of the plant species which serves as host for the larvae.

The cotton-boll weevil *Anthonomus grandis,* fig. 319, is one of the most serious cotton pests in the United States and is high on the list of insects causing excessive commercial damage. The adults attack

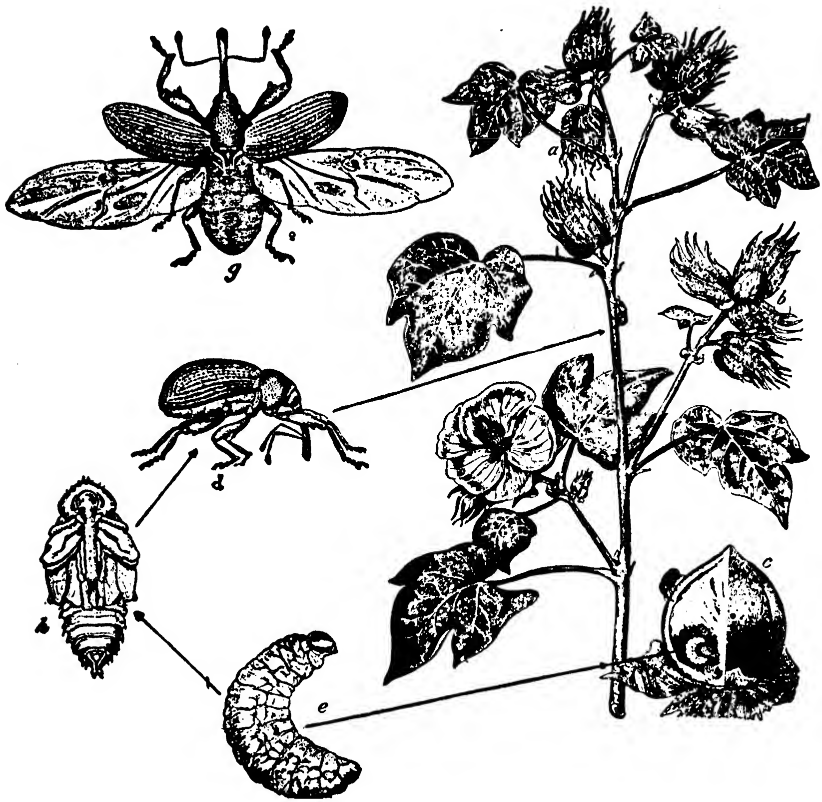


FIG 319. The cotton boll weevil *Anthonomus grandis*. On the right a cotton plant attacked by the boll weevil, showing at *a,* a hanging dry infested square; at *b,* a flared square with weevil punctures; at *c,* a cotton boll sectioned to show attacking weevil and larva in its cell; *g,* adult female with wings spread as in flight; *d,* adult from the side; *h,* pupa ventral view and *e,* larva. (From Metcalf and Flint, "Destructive and Useful Insects," by permission of McGraw-Hill Book Co.)

the plants first in the season, feeding on the leaves and in the flowers and young bolls. The females deposit their eggs in feeding holes in the bolls, one egg to each hole. The larvae feed inside the boll, thus making a cell in which they pupate. Adults emerge in a few weeks, cause additional damage by their feeding, and then go into hibernation at the onset of winter. The boll weevil is a native of tropical America and entered Texas from Mexico about 1890. Since that time it has spread gradually throughout most of the cotton-growing region of the United States.

The plum curculio *Conotrachelus nenuphar,* fig. 320, attacks plums, cherries, and related fruits; the larvae feed in the body of the fruit. This species is frequently a serious pest.

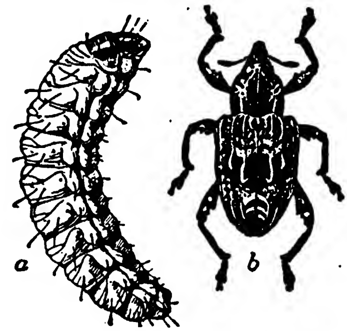


FIG. 320. The plum curculio *Contrachelus nenuphar.* *a,* larva; *b,* adult. (From U.S.D.A., B.E.P.Q.)

Of especial importance to stored grains are the granary weevil *Sitophilus granarius* and the rice weevil *Sitophilus oryzae;* the larvae of both species live and feed inside grain kernels, and the adults feed either in the old larval burrows or promiscuously on the grain.

Scolytidae, the Bark Beetles. The species of this family feeds chiefly in trees, either alive or dead. The beetles have only an indistinct snout and are almost cylindrical in body shape, fig. 321. The larvae are legless grubs with typical weevil characteristics. Both adults and larvae feed in galleries, fig. 322. In some species these galleries are in the

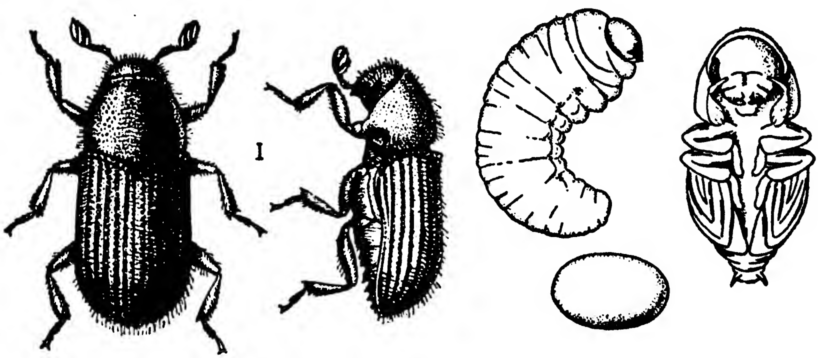


FIG. 321. The peach bark beetle *Phlœotribus liminaris.* (From U.S.D.A., B.E.P.Q.)

cambium layer of the tree and if sufficiently numerous result in girdling the tree. Many species of this family attack commercial timber, especially pine, and sometimes cause the premature death of large stands of it.

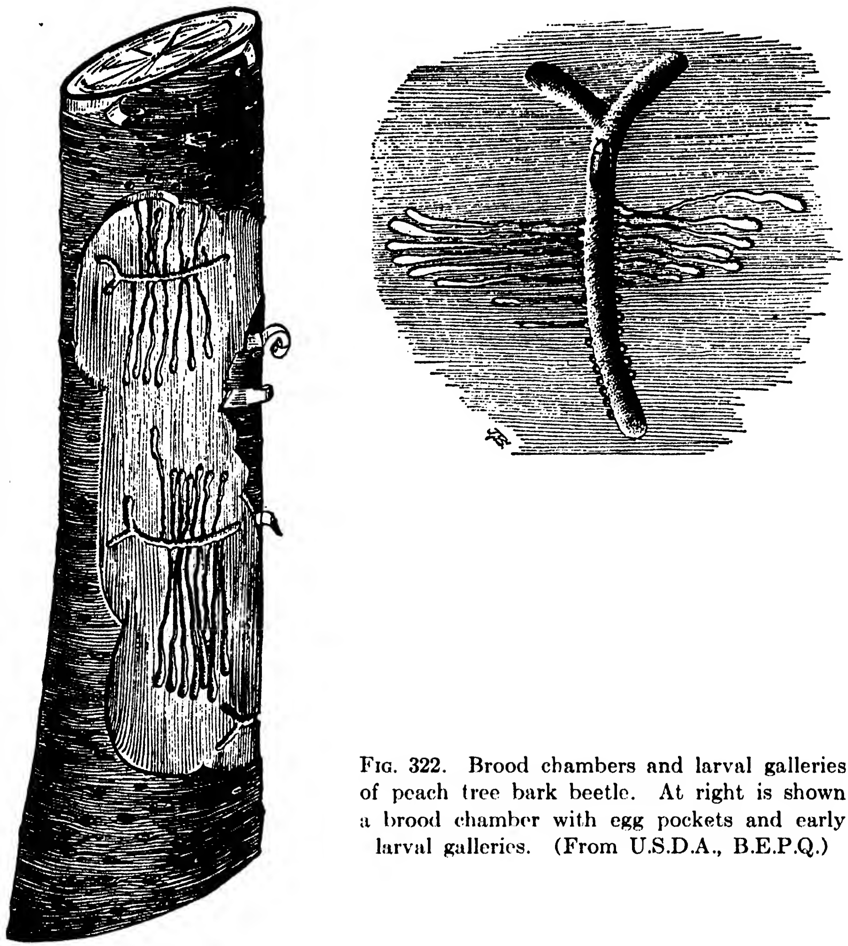


FIG. 322. Brood chambers and larval galleries of peach tree bark beetle. At right is shown a brood chamber with egg pockets and early larval galleries. (From U.S.D.A., B.E.P.Q.)

Suborder STREPSIPTERA

This suborder, fig. 323, comprising the stylopids or twisted wing flies, is truly the most remarkable group of the Coleoptera, combining extreme specialization in parasitic habits with equal specialization in structure. It contains two families, the Stylopidae and Mengeidae, both seen only rarely by the collector.

Stylopidae. The male is winged and free flying, more like a fly than a beetle, its elytra reduced to twisted finger-like organs, the hind wings large and fan-shaped, and the metathorax greatly enlarged. The antennae are short and have at least some leaflike segments; the eyes are berry-shaped, with each ommatidium protruding and dis-

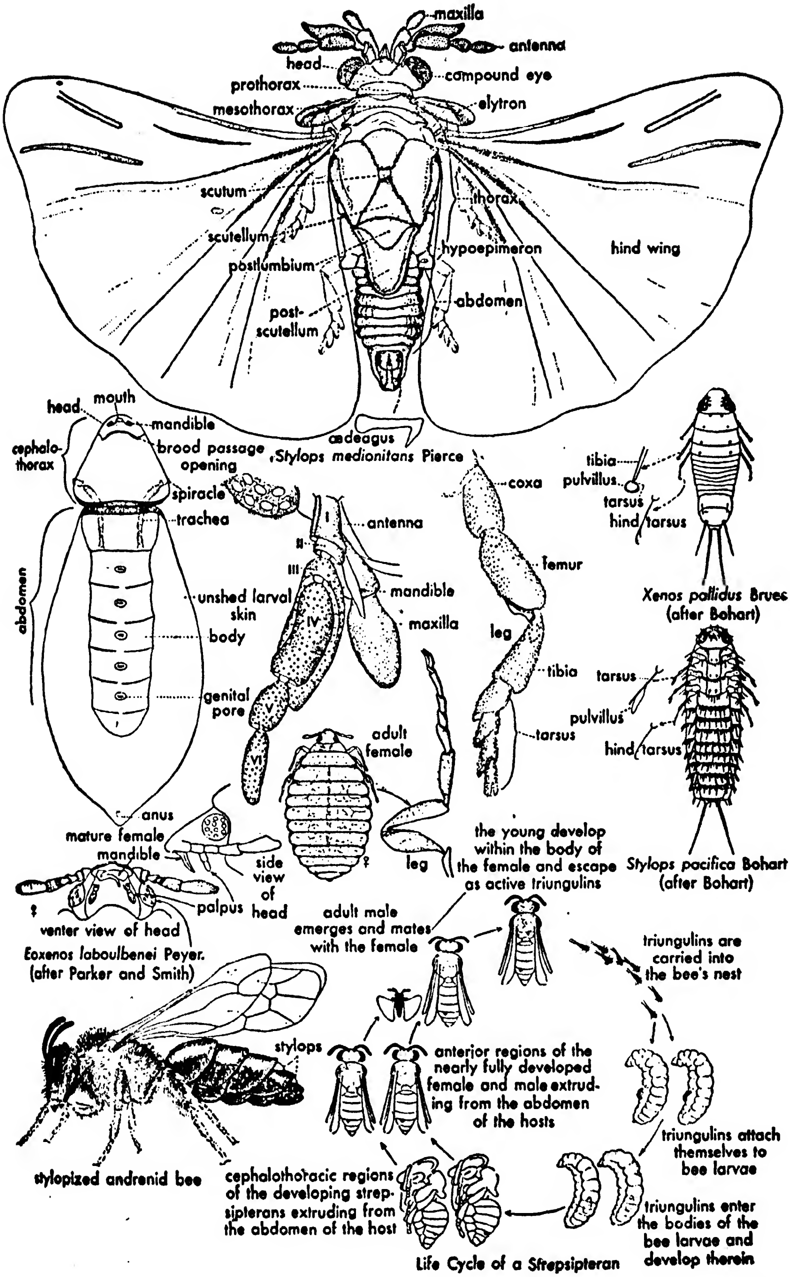


FIG. 323. Strepsiptera, important characteristics and life cycle. (From Essig. "College Entomology," by permission of The Macmillan Co.)

tinct. The female is extremely degenerate, being only a sac enveloped by the last larval skin; it remains embedded in the host, with only an anterior portion, called a cephalothorax, projecting on the outside of the host integument.

The female is viviparous; the first-instar larvae develop inside her body and escape to the outside by crawling through a slit in the exposed cephalothorax. These larvae, called triungulinids because of their similarity to meloid triungulins, are curious active creatures, having three pairs of legs, well-developed sclerites, reduced mouthparts and ocelli, several well-developed eye facets, and one or two pairs of long terminal filaments. The larvae can run and jump with great agility. Each attaches and burrows into an individual host and soon molts into a legless grub. The grub lies quiescent in the host body and absorbs its food by diffusion from the host blood stream. Thus there is no actual destruction of tissues like that caused by the usual type of insect parasitic larva which macerates and ingests its food by mouth. When full grown, the stylopid larva pushes its anterior end between the abdominal sclerites of the host so that the head and thoracic region is exposed, forming a round or flattened structure. If the larva is a male, it transforms within the larval skin to a typical beetle pupa; when mature, the adult breaks through the exposed larval skin and escapes to the outside. If the larva is a female, it has no definite pupal stage, molting directly into the sac-like adult female which remains within the larval skin. The eggs develop and hatch within the body of the mother, until she is merely a sac of eggs or young. The number of progeny of one of these females is enormous; counts of young range from twenty-five hundred to seven thousand per female.

The North American species of stylopids attack chiefly various groups of bees and wasps. In other parts of the world different groups of stylopids attack Hemiptera (Cicadellidae, Fulgoridae, and certain allied families) and Orthoptera.

The closely allied family Mengeidae is similar in most respects to the Stylopidae, but has a free-living larviform female. The host of the only nearctic genus is unknown, but European species parasitize silverfish.

The Stylopidae and their close allies are regarded by some authors as comprising a separate order, the Strepsiptera. Most workers agree, however, that this group originated with the beetle complex. The triungulinid larva, reduced wing venation, and parasitic habit suggest a relationship near the Meloidae.

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Order TRICHOPTERA

Caddisflies

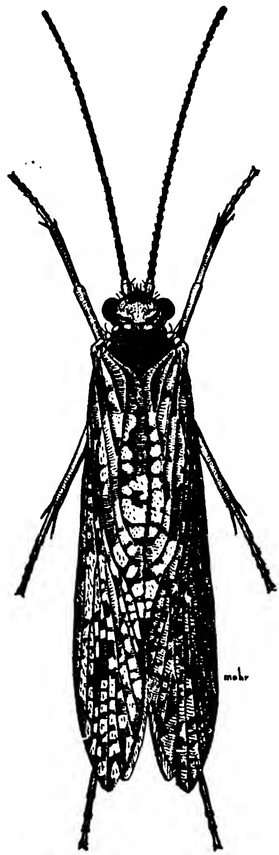

FIG. 324. A caddisfly *Rhyacophila fenestra.* (From Illinois Natural History Survey)

Mothlike insects, having aquatic larvae and pupae. The adults, figs. 324, 325, vary in length from 1.5 to 40 mm. They have chewing-type mouthparts, with all parts greatly reduced or subatrophied except for the two pairs of palpi; long multisegmented antennae; large compound eyes; and long legs. Except for the wingless or brachypterous females of a few species, the adults have two pairs of large membranous wings, with a fairly complete set of longitudinal veins, but a reduced number of crossveins. In most species the body and wings have hair but no scales; in a few species the antennae, palpi, legs, and wings may have patches of scales or a scattering of scales among the longer hair. The larvae, figs. 326 and 327, are diverse in general appearance and habits. The eyes are each represented by a single facet, the antennae are small and one-segmented, the mouthparts are of the chewing type and well developed. The thorax has three pairs of strong legs, the abdomen a pair of strong anal legs bearing hooks and frequently a set of finger-like gills.

Most of the adults are somber in color or tawny, but a few have wings which are marked with yellow or orange, fig. 325, or have silvery streaks.

Caddisfly larvae live in both lakes and streams, showing a definite preference for colder and unpolluted water. As a group they have a wide ecological tolerance but a more restricted one than midge larvae (Chironomidae) in relation to pollution.

Casemaking has been developed to a high degree by the larvae of most families of these insects. The cases, which are portable "houses"

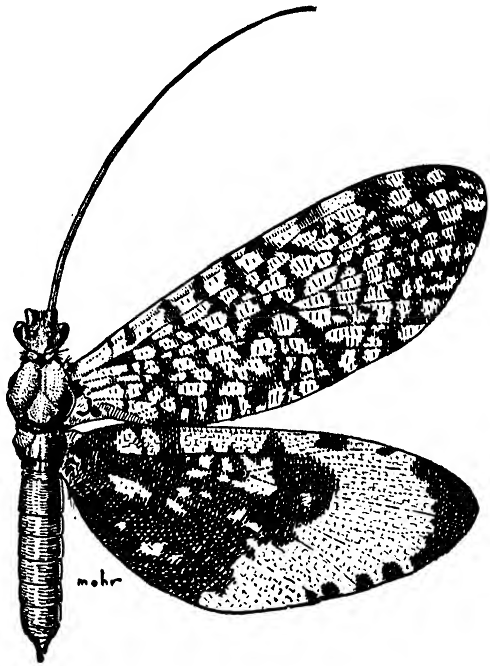

FIG. 325. *Eubasilissa pardalis,* one of the more showy nearctic caddisflies. (From Illinois Natural History Survey)

built by the larvae, have fascinated observers of fresh-water insect life. Cases, figs. 328, 329, are of varied shapes, ranging from a straight tube to the coiled case of *Helicopsyche,* which resembles a snail shell, fig. 330. Many types of materials are used in the construction of these cases. Small stones, sand grains, bits of leaves, sticks, conifer needles, and frequently small snail shells may be utilized. In most instances a given genus or species constructs a case of characteristic shape, but genera in different families often make very similar cases.

Caddisfly females lay from three hundred to one thousand eggs each. In some species the eggs are discharged in strings, fig. 331*B;* the female enters the water and lays the eggs on stones or other objects, grouping the strings into irregular masses containing up to eight hundred eggs. Females of other groups extrude the eggs and form them into a large mass at the tip of the abdomen before depositing them, fig. 331*A*. The eggs are incased in a gelatinous matrix which swells on absorbing moisture. These masses are attached to sticks or stones which are submerged in, adjacent to, or overhanging water.

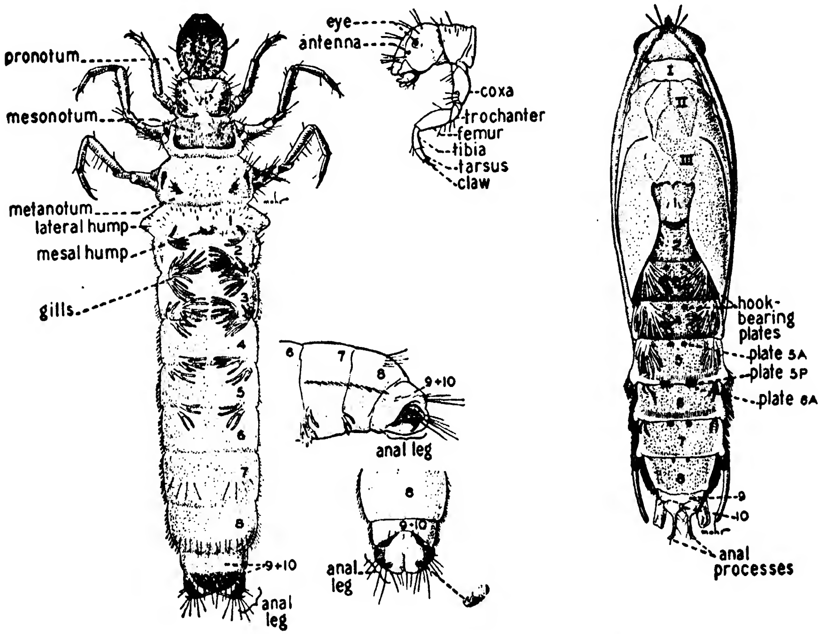

FIG. 326. Larva and pupa of a casemaking caddisfly *Limnephilus submonilifer*. (From Illinois Natural History Survey)

Females of the family Limnephilidae frequently deposit egg masses on branches overhanging water. On numerous occasions observers have reported that these egg masses swell and liquefy, and the eggs hatch during rain. The gelatinous drops formed by this process run down the twigs and drop into the water, carrying the larvae along.

The larvae are all active, most of them feeding chiefly on small aquatic animals or microorganisms which encrust decayed organic matter in the water. A few genera, notably *Rhyacophila* and *Oecetis*, are predominantly predaceous, feeding on small insect larvae. Larvae of the genus *Rhyacophila*, fig. 324, are free living, constructing no larval case. Three families, the Philopotamidae, Psychomyiidae, and

Hydropsychidae, have larvae that weave a fixed net and shelter, the net presumably being used to trap small aquatic organisms which constitute their food. In all other families the larvae construct portable cases of various types. The larva uses these to protect the

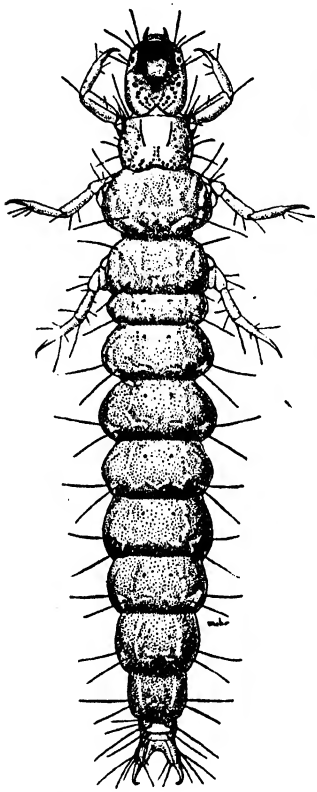

FIG. 327. Free living caddisfly larva *Rhyacophila fenestra.* (From Illinois Natural History Survey)

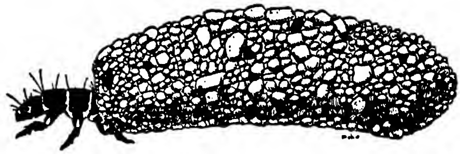

FIG. 328. Purselike caddisfly case and larva, *Ochrotrichia unio.* (From Illinois Natural History Survey)

FIG. 329. Caddisfly larva in cylindrical case, *Limnephilus rhombicus.* (From Illinois Natural History Survey)

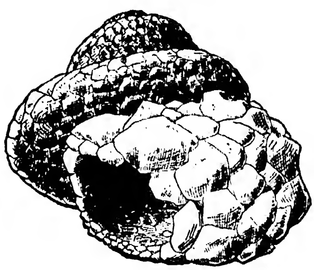

FIG. 330. The snaillike case of *Helicopsyche.* (From Illinois Natural History Survey)

greater part of the body, which has thin integument. Only the heavily sclerotized head, legs, and anterior portion of the thorax are extruded from the case when the larva is actively moving about, figs. 328, 329.

Prior to pupation, the larvae of all caddisflies spin a cocoon. The casemakers form this very simply by spinning a silken lining inside the case and closing the ends of the case with a barred or slit mem-

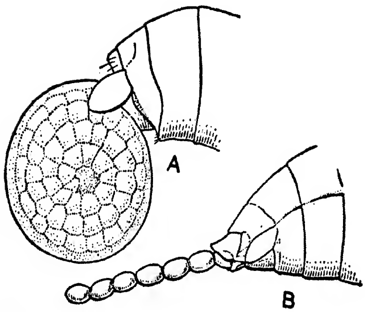

FIG. 331. Caddisfly eggs. *A*, *Triaenodes tarda*; *B*, *Cyrnellus marginalis*. (From Illinois Natural History Survey)

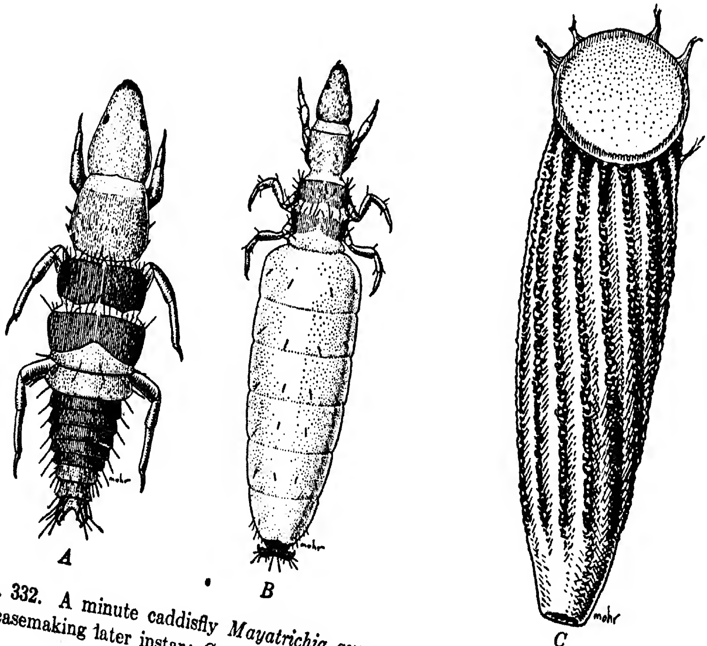

FIG. 332. A minute caddisfly *Mayatrichia ayama*. *A*, free living, early instar; *B*, casemaking later instar; *C*, case closed for pupation. (From Illinois Natural History Survey)

brane. The free-living and net-making species spin an ovoid cocoon of silk and sand, stones, or bits of debris, which is firmly attached to a stone, log, or other rigid support. The pupae develop in the cocoon until the adult structures (except wings) are completely formed and fully sclerotized. The pupae, fig. 326, are unusual in possessing strong mandibles. With these, the mature pupa cuts its way out of the cocoon. It then swims to the surface, crawls on a log or stone, and transforms into an adult.

Usually the complete life cycle requires a year, most of it spent in the larval stage. The egg stage lasts only a short time; the pupal stage requires 2 to 3 weeks; and the adults live about a month.

Of interest among caddisflies are the larval habits of "micro" caddisflies, or Hydroptilidae. This family contains only small individuals, ranging from 1.5 to 6 mm. in length. The first instars are minute free-living forms, with small abdomens; the later instars build portable cases and have swollen abdomens. Information is available only on two North American genera, *Mayatrichia,* fig. 332, and *Ochrotrichia.* In the latter there are differences in the structure of the claws between the free-living and casemaking instars. This dimorphism is similar in many respects to typical examples of hypermetamorphosis.

The caddisfly fauna of the nearctic region contains over eight hundred species grouped in seventeen families.

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Order LEPIDOPTERA

Moths and Butterflies

Insects with two pairs of wings, fig. 333, except for a few species which have apterous females. The body, wings, and other appendages are covered with scales which are often brilliant in color and arranged in showy patterns. Adult mouthparts are greatly reduced; in most forms only the maxillae are well developed. These are fused and elongated to form a coiled tube for sucking up liquid food. The large compound eyes, the long antennae, and the legs are all well developed. The species have complete metamorphosis. The larvae, fig. 346, are cylindrical (the familiar caterpillars); most of them have a definite head, thoracic legs, and five pairs of larvapods (including the end pair). The pupae are usually hard and brown, and the appendages appear cemented onto the body.

The order is a large one, embracing about ten thousand North American species. The adults of these vary greatly in size from minute forms a millimeter or two long to large species with a wing

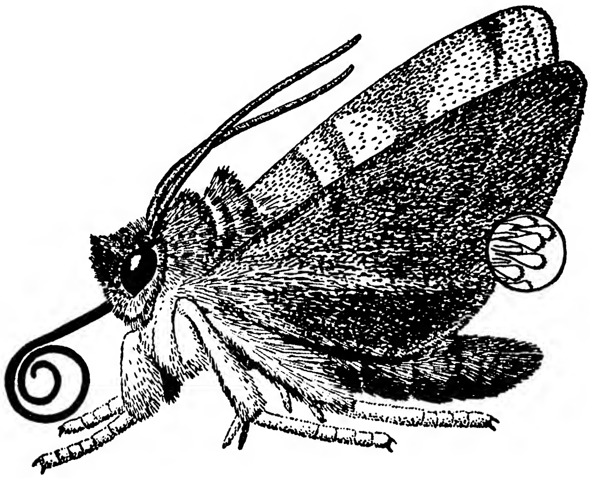

Fig. 333. A typical moth, showing scales on wings and body, and sucking tube which is coiled under head when not in use. (From Illinois Natural History Survey)

span of 6 inches or more. The wings are distinctively patterned, and the order as a whole presents an attractive array of color and beauty.

The larvae of the Lepidoptera are plant feeders except for a scattering of species which are predaceous, scavengers, or feed on stored products. The great bulk of the species feed externally on foliage; a large number of the minute species mine inside leaves or leaf petioles; and another large group, including both large and small species, bore inside stems, trunks, or roots. A great number of these species attack cultivated plants and cause a high annual loss of crops and stored products. The order is therefore one of great economic importance.

In addition to its destructive species, the order Lepidoptera contains one of great commercial value—the silkworm *Bombyx mori*. This insect is the sole source of natural silk. The propagation of the species and the harvesting of the silk, known as sericulture, is an important industry in many parts of the world, with an annual harvest in oriental countries of many million dollars' worth of silk. At the turn of the century a sericulture industry was established in California. This failed because of high labor costs. In 1945 a new venture was started in Texas in which a large part of the work was done mechanically.

Key to Suborders and Common Families

1. Wings reduced to small pads or entirely lacking, fig. 350 2
   Wings well developed, at least nearly as long as abdomen, fig. 337 4

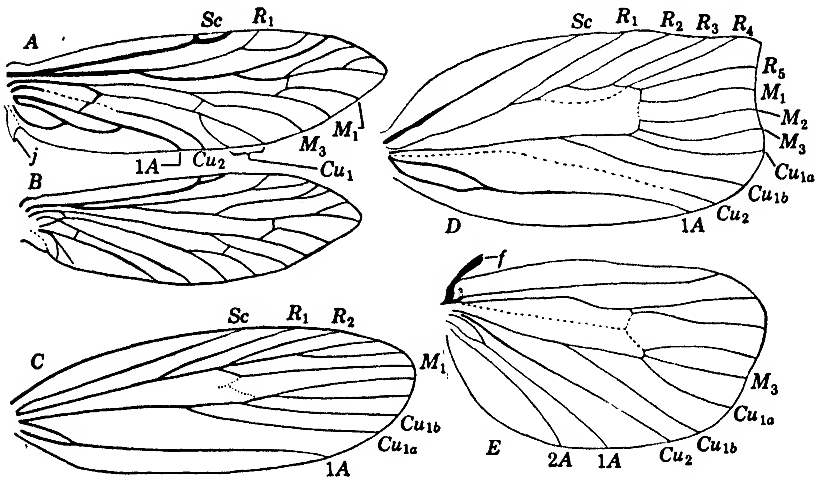

Fig. 334. Wings of Lepidoptera. *A* and *B*, front and hind wings of *Mnemonica*, Eriocraniidae; *C*, front wing of *Achroia*, Pyralidae; *D* and *E*, front and hind wings of *Archips*, Tortricidae. *f*, frenulum; *j*, jugum. (*C* loaned by Dr. Kathryn M. Sommerman)

2. Legs lacking or reduced to short stubs; usually associated with a baglike case, fig. 339 .... **Psychidae,** p. 380
   Legs elongate and normal in appearance 3
3. Abdomen having closely set scales or spines, or bristling dark-gray hair; usually not found near cocoon .... **Geometridae,** p. 389
   Abdomen smoothly clothed with fine light woolly hair; moth usually found clinging to cocoon .... **Liparidae,** p. 391
4. Front wing having a *jugum*, a lobe at the base of the posterior margin for use in wing coupling, fig. 334*A*; front and hind wings similar in venation and shape (**Jugatae**) .... **Hepialidae,** p. 378
   Front wing without a jugum; anterior margin of hind wing having an enlarged lobe at base, fig. 336*D, H, I*, or with a long basal spine, or *frenulum*, fig. 334*E*, both used for wing coupling; front and hind wings usually markedly different in shape or venation 5

5. Hind wing without a frenulum, and antenna clubbed or hooked at apex, fig. 335*E*, *F* (**Rhopalocera**) 6
   Either hind wing having a frenulum, or antenna not clubbed or hooked; instead either threadlike, or serrate, or pectinate (**Frenatae**) 10
6. Front wing having each of the 5 branches of radius and 3 of media arising from the discal cell, fig. 335*A*; antennae usually hooked at apex, fig. 335*F* **Hesperiidae**, p. 394

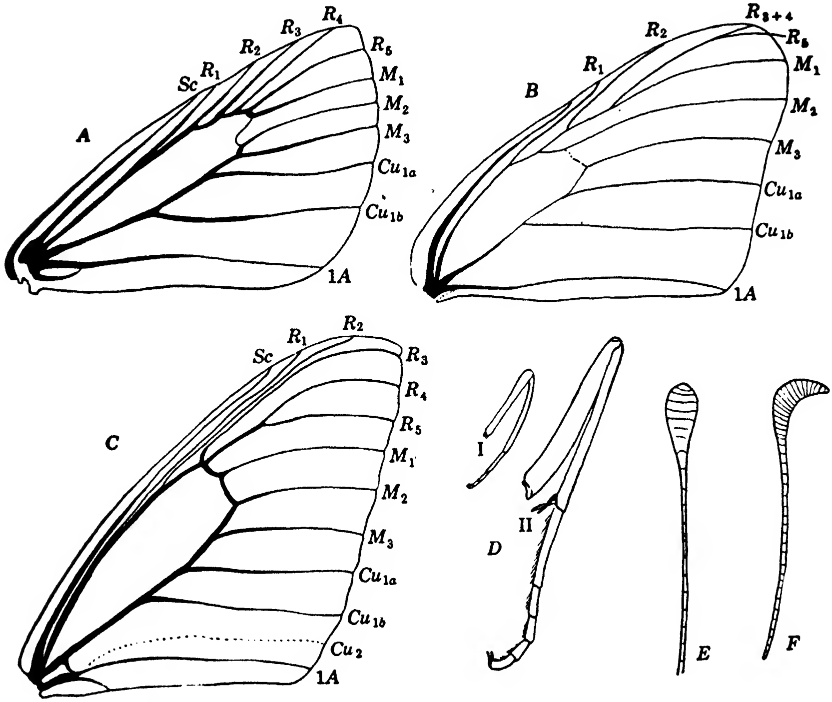

FIG. 335. Diagnostic parts of Lepidoptera. *A*, front wing of *Pamphila*, Hesperiidae; *B*, front wing of *Pieris*, Pieridae; *C*, front wing of *Papilio*, Papilionidae; *D*, front (small) and middle legs of *Brenthis*, Nymphalidae; *E*, tip of antenna of same; *F*, tip of antenna of *Thanaos*, Hesperiidae.

   Front wing having some of these fused at base, branching beyond discal cell, fig. 335*B*, C 7
7. Front wing having Cu_1 appearing 4-branched, fig. 335*C*, because both M_2 and M_3 are more closely associated with it than with R_5 . . . . **Papilionidae**, p. 394
   Front wing having Cu_1 appearing 3-branched, fig. 335*B*, because M_2 is more closely associated with R_5 8
8. Front legs reduced, and much shorter than the other legs, fig. 335*D* **Nymphalidae**
   Front legs larger in proportion to the others 9

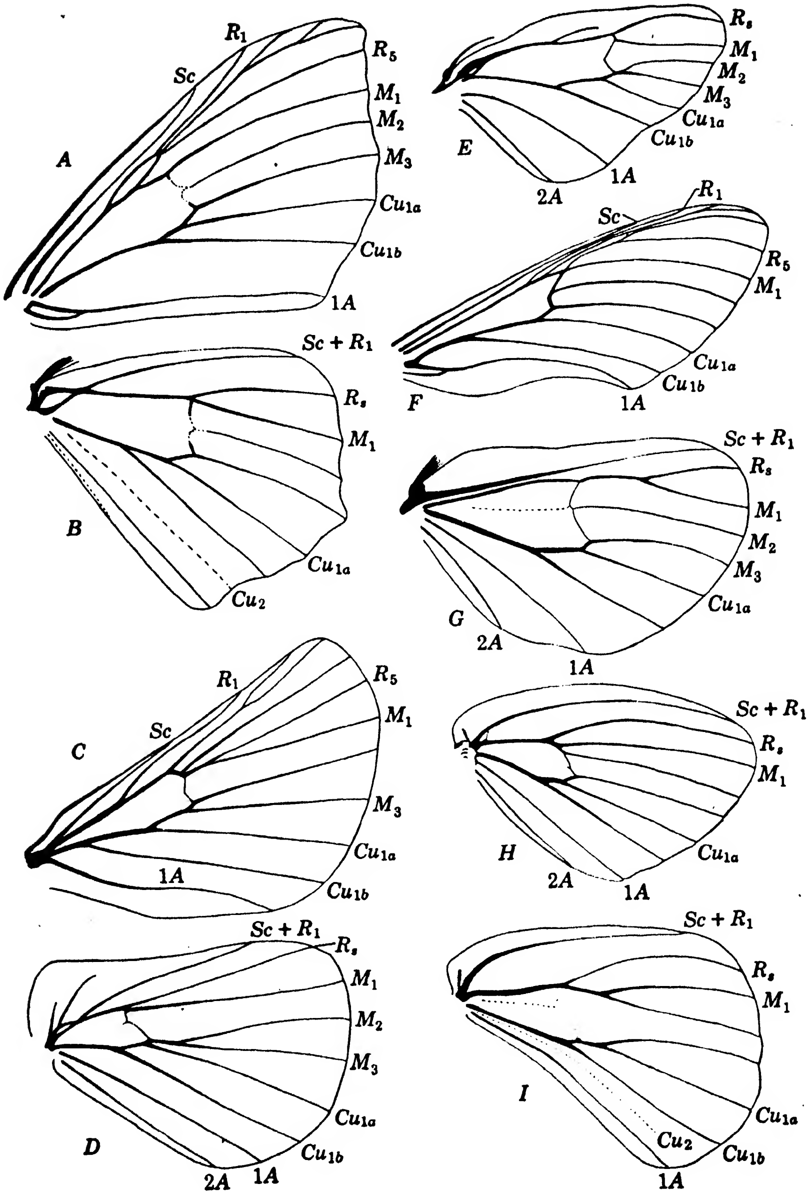

FIG. 336. Wings of Lepidoptera. *A, B,* front and hind, *Acidalia,* Geometridae; *C, D,* front and hind, *Malacosoma,* Lasiocampidae; *E,* hind, *Halisidota,* Arctiidae; *F,* front, *Protoparce,* Sphingidae; *G,* hind, *Hyperaeschra,* Notodontidae; *H,* hind, *Citheronia,* Citheroniidae; *I,* hind, *Samia,* Saturniidae.

9. Front wing having M_1 fused for a considerable distance with posterior branch of radius, fig. 335*B*; colors white, yellow, or orange, plus black marks
Pieridae, p. 394
Front wing having M_1 either not fused with *R*, or only slightly so, thus arising from discal cell or very near it; colors coppery, blue, or brown... **Lycaenidae**
10. Hind wing having a posterior fringe as long as wing is wide, fig. 337; wing usually lanceolate. A large number of families of small moths difficult to identify, including Yponomeutidae, Gelechiidae, and Tineidae
Not keyed further here
Hind wing wider than its fringe 11

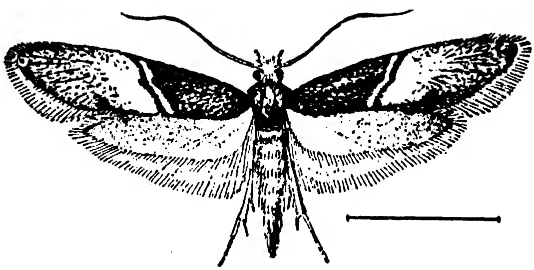

FIG. 337. The tapestry moth *Trichophaga tapetzella,* one of the Microlepidoptera. (From U.S.D.A., B.E.P.Q.)

11. Front wing narrow, more than four times as long as wide; hind wing and sometimes front wing having transparent areas devoid of scales, fig. 343
Aegeriidae, p. 381
Front wing wider, hind wings usually entirely covered with scales 12
12. Hind wing having 3 veins posterior to Cu_{1b}, fig. 334*E* 13
Hind wing having 1 or 2 veins posterior to Cu_{1b}, fig. 336*E* 14
13. Front wing with Cu_2 fairly well developed, at least towards apex, fig. 334*D*
Tortricidae, p. 384
Front wing with Cu_2 atrophied, fig. 334*C* .... **Pyralidae,** p. 384
14. Front wing with 1*A* evenly bowed anteriorly, the vein coming close to central portion of Cu_1 or apex of Cu_{1b}, fig. 336*F* .... **Sphingidae,** p. 387
Front wing with 1*A* straight or only slightly sinuate, fig. 336*C* 15
15. Front wing having both M_2 and M_3 associated closely with Cu_1, which therefore appears 4-branched, fig. 336*C* 16
Front wing having M_2 either midway between M_3 and R_5, or closer to R_5, so that Cu_1 appears 3-branched, fig. 336*A* 19
16. Hind wing without a frenulum, the base of the front margin greatly expanded. fig. 336*D* .... **Lasiocampidae,** p. 386
Hind wing with a frenulum 17
17. Hind wing having $Sc + R_1$ and R_s fused for about half length of discal cell, then the two veins separating, fig. 336*E* .... **Arctiidae,** p. 393
Hind wing having $Sc + R_1$ fused with R_s for only a short distance, or the veins not at all fused 18
18. Head having two ocelli .... **Noctuidae,** p. 392
Head without ocelli .... **Liparidae,** p. 391

19. Hind wing having $Sc + R_1$ arcuate, curving forward from its base and well separated from R_s for its entire distance, fig. 336*H*, *I*; frenulum obsolete . . 20
Hind wing having $Sc + R_1$ either fused for a distance with R_s, fig. 336*B*, or running close to it, fig. 336*G*; frenulum present, often tuftlike 21
20. Hind wing having two anal veins, fig. 336*H* . . . . **Citheroniidae**, p. 390
Hind wing having only one anal vein, fig. 336*I* . . . . **Saturniidae**, p. 390
21. Hind wing with *Sc* making a short sharp angulation at the base of the wing, fig. 336*B* . . . . **Geometridae**, p. 389
Hind wing with *Sc* not angulate at base, fig. 336*G* . . . . **Notodontidae**

Suborder JUGATAE

The Jugatae are the most primitive present-day Lepidoptera. In addition to possessing a jugum, adults of this suborder have front and hind wings of very similar shape and venation. In one group the pupae have long stout mandibles used for cutting an exit from the cocoon; the adult mouthparts include well-developed mandibles and lobelike maxillae and labium, which are not elongated and appressed to form the usual sucking tube. These characters are of great interest, because they are also found in the Trichoptera, and they demonstrate the close relationship between primitive members of the Trichoptera and of the Lepidoptera.

The Jugatae are represented in North America by only a few species. The family Micropterygidae has mandibulate adults of small size; its larvae feed on moss. The Eriocraniidae also includes small species but these have vestigial mandibles and a sucking tube; the larvae are leaf miners. The Hepialidae includes a few larger species (with a wing expanse up to 2 inches) called swifts because of their rapid flight; their larvae are wood borers or root feeders.

Suborder FRENATAE

Here belong the greater number of the Lepidoptera, representing a great variety of shapes, sizes, and habits. The adult, in addition to lacking a jugum, has hind wings which differ in shape from the front ones, and which also have the radial sector usually reduced to a single vein; in the front wings the radial sector usually has three or four branches. The pupa is obtect; that is, the appendages appear embedded in the body of the pupa and are incapable of movement.

In North America we have fifty families represented, many of them containing species of great economic importance. The diagnosis and identification of these families are difficult and require making special preparations of the wings after their scales have been removed, a process known as denuding.

The "Micros"

Many families of the Frenatae comprise small slender moths having the hind wings either with vein 1*A* present, or bearing a long posterior

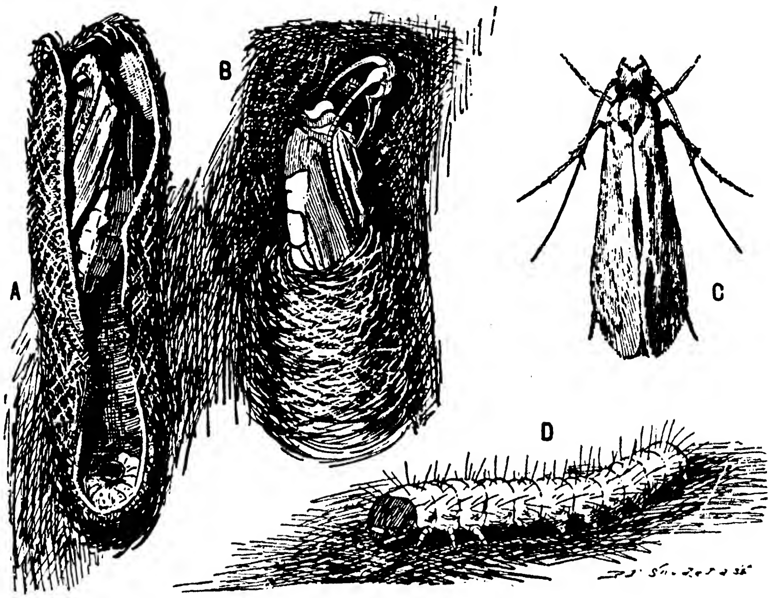

FIG. 338. The clothes moth *Tinea pellionella*. *A*, cocoon cut open showing fully formed pupa within; *B*, empty pupal skin projecting from door of cocoon after the moth has emerged; *C*, adult moth; *D*, the larva which does the damage to clothes. (After Snodgrass)

fringe, or extremely narrow and pointed in outline. These are frequently termed the Microlepidoptera. Most of them belong to the group called the Microfrenatae. A few members of the Microfrenatae are quite large, so that size is only an average characteristic for the group. Although it is impractical to give defining characters for them here, a few families are mentioned which contain common species of importance.

Tineidae. The larvae feed chiefly on fungi or fabrics, or as scavengers. Included in the Tineidae are our common clothes moths, fig. 338. The webbing clothes moth *Tineola bisselliella* has a larva which makes an indefinite web; in addition to fabrics, it has a marked liking for old feathers. The larva of the casemaking clothes moth *Tinea pellionella* makes a portable case of silk and fabric fragments. Both species are common pests of fabrics of animal origin, such as wool, furs, and feathers.

Psychidae, the Bagworms. This family has relatively large species, some attaining a wing spread of 30 mm. The larvae construct a case

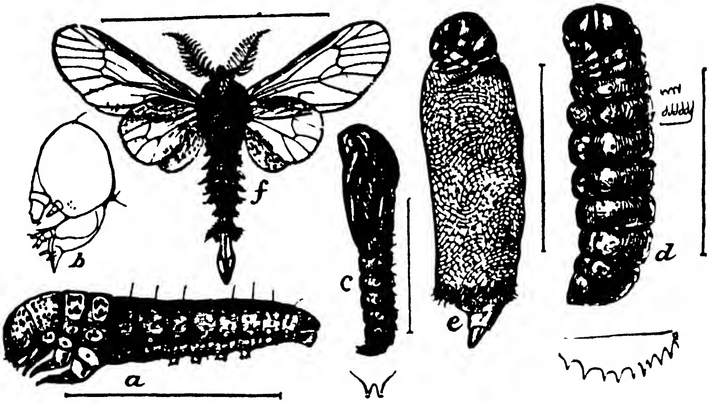

FIG. 339. Stages in the life cycle of the bagworm *Thyridopteryx ephemeraeformis*. *a*, full-grown larva; *b*, head of same; *c*, male pupa; *d*, female pupa; *e*, adult female; *f*, adult male. (From U.S.D.A., B.E.P.Q.)

or bag of silken fabric and bits of leaf or bark, fig. 339. Only the heavily sclerotized head and thorax project from the case. These bags are a familiar sight hanging from the twigs or leaves of many species of coniferous and deciduous trees. The common bagworm in the eastern states is *Thyridopteryx ephemeraeformis*, fig. 340. The males have fuzzy dark bodies, pectinate antennae, and usually clear wings. The females are larviform and have almost lost the power of locomotion. The life history has some peculiarities. By late summer the larva is full grown, whereupon it fastens its bag to a twig and pupates inside the bag. When mature, the male pupa emerges partially out of the bag, and the adult male emerges from it in this position. The female pupa stays within the bag; the female adult works itself partway out of the pupal skin and awaits fertilization. The males fly about looking for bags containing mature females and mate with them by means of an elongate extensile copulatory apparatus that can be extended deep into the bag containing the female. Soon after fertilization the female lays eggs, simply allowing them to fall into her old pupal skin, which becomes half filled with them. This completed, the spent female crawls out of the bag, falls to the ground, and dies. The eggs lie dormant over winter and hatch the next spring. The newly hatched larvae crawl out of the old bag, disperse, and begin feeding.

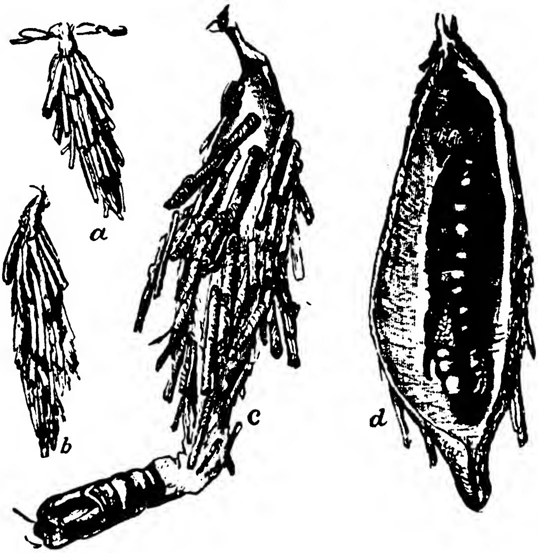

FIG. 340. Bagworms at successive stages (*a, b, c*). *c*, male bag; *d*, female bag. (From U.S.D.A., B.E.P.Q.)

Gelechiidae. The larvae of this family exhibit a wide diversity of food and hosts. Several eastern species of *Gnorimoschema* make large stem galls, fig. 341, on goldenrod and related Compositae; the larva feeds within the galls and when full grown pupates there. The pink bollworm *Pectinophora gossypiella* tunnels through the developing cotton boll and feeds on the seeds. It is a native of Asia that has spread to all the cotton-growing regions of the world and is one of the worst pests of this crop. Also included in the family are species which mine the needles of pine and other conifers and attack potatoes, fig. 342, and tomatoes, and some which bore in twigs and fruits of certain trees. One species is a world-wide pest of stored grain, the Angoumois grain moth *Sitotroga cerealella.*

Aegeriidae, the Clear-Wings. These are moderate-sized narrow-winged forms in which the front and hind wings are coupled by a series of interlocking spines situated near the middle of the wing margins. In most species the wings have definite window-like areas free from scales; hence the name "clear-wing" moths. The adults

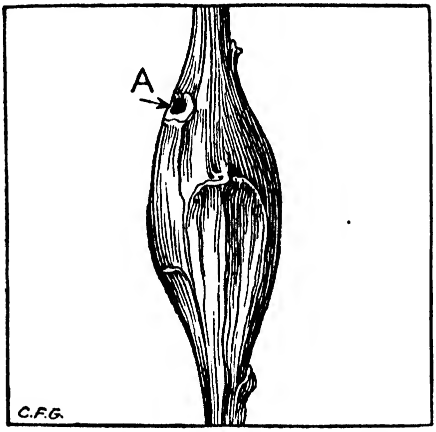

Fig. 341. Goldenrod gall of *Gnorimoschema gallaesolidaginis.* (From Chicago Museum of Natural History)

are diurnal and extremely rapid in flight, and in many the body and wings are banded with purple, red, and yellow, apparently mimicking some of the common wasps. The larvae are stem borers, attacking

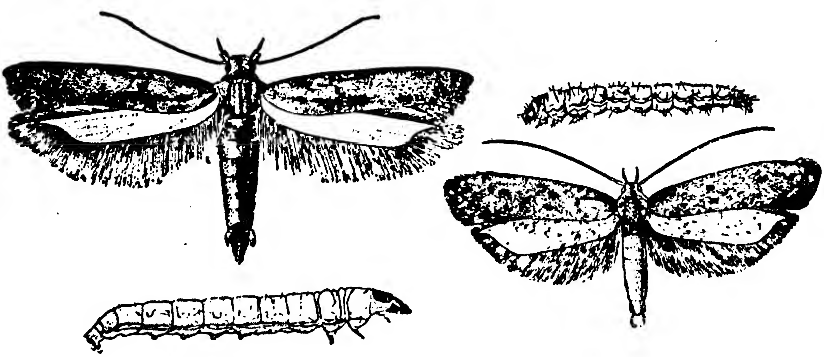

Fig. 342. Left, the potato tuber moth *Gnorimoschema operculella;* right, the eggplant leaf miner *G glochinella.* (From U.S.D.A., B.E.P.Q.)

herbs, shrubs, and trees. Two of notable economic importance are the peach tree borer *Sanninoidea exitiosa,* fig. 343, and the squash borer *Melittia cucurbitae,* fig. 344.

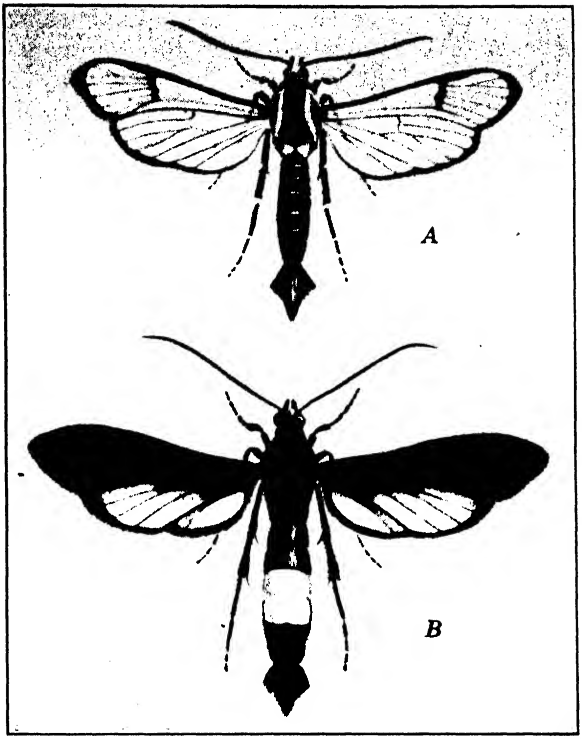

FIG. 343. The peach tree borer *Sanninoidea exitiosa*. *A*, male; *B*, female. (From U.S.D.A., B.E.P.Q.)

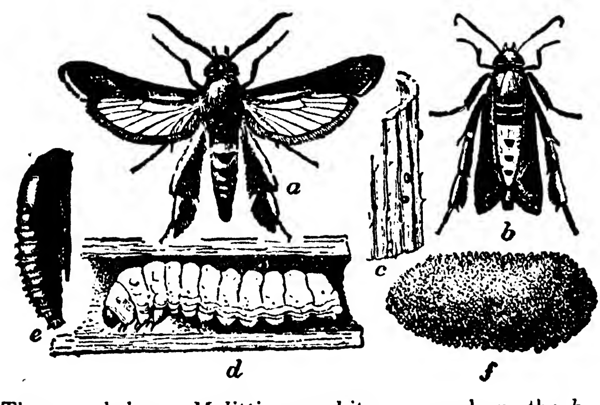

FIG. 344. The squash borer *Melittia cucurbitae*. *a*, male moth; *b*, female with wings folded; *c*, eggs on stem; *d*, larva; *e*, pupa; *f*, pupal cell. (From U.S.D.A., B.E.P.Q.)

Tortricidae. A very large family of small to medium-sized moths, having wide wings, the front pair with the apical margin truncate or even concave or excised. The larvae feed on nuts, fruits, and leaves, and in stems. In many species the larvae make nests by rolling and tying leaves, from which they get their common name, leaf rollers. The group includes the red-banded leaf roller *Argyrotaenia velutinana,* fig. 345, which feeds on many wild and cultivated trees and shrubs. Some other economic species in the family are the oriental fruit moth *Grapholitha molesta,* which feeds in the twigs and fruits of peaches,

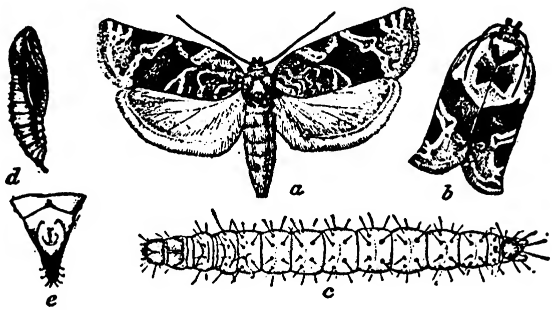

FIG. 345. The red-banded leaf roller *Argyrotaenia velutinana.* *a, b,* moth; *c,* larva; *d,* pupa; *e,* tip of pupal abdomen. (From U.S.D.A., B.E.P.Q.)

plums, and related fruit trees; the pine shoot moths, several species of *Rhyacionia,* which destroy the terminal buds of pine; and the grape berry moth *Polychrosis viteana,* which feeds on the leaves and in the fruits of grapes.

Pyralidae. This is a large family, economically one of the most important in the order. In taxonomic position the pyralids are intermediate in many characters between the "micros" and the "macros." The moths vary greatly in size and shape, but are usually delicate, trim, and have a rather detailed and soft coloration pattern. The larvae exhibit a wide range of food habits: feeding on leaves, fruits, and flowers; boring in stems or stalks; some being saprophagous and a few predaceous. Many spin an extensive web over their food and surroundings and are called webworms, such as the garden webworm *Loxostege similalis,* fig. 346. The family includes some of the most troublesome pests of agricultural crops. The European corn borer *Pyrausta nubilalis* and the southwestern corn borer *Diatraea grandiosella* are serious pests of corn; the greenhouse leaf tier *Phlyctaenia rubigalis* is a pest of chrysanthemums and other greenhouse crops;

the wax moth *Galleria mellonella* is often a serious pest of beehives. Several species, including the Indian-meal moth *Plodia interpunctella,*

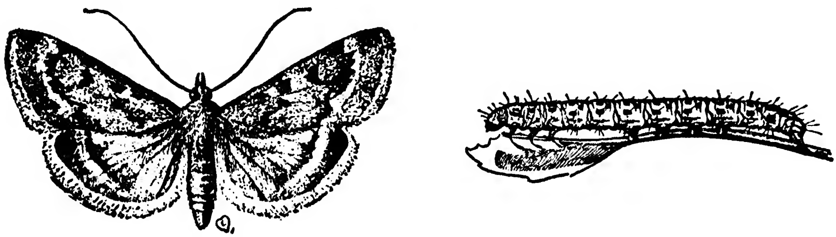

FIG. 346. The garden webworm *Loxostege similalis,* adult and larva. (From U.S.D.A., B.E.P.Q.)

attack stored grain and prepared foods, and *Ephestia elutella,* fig. 347, feeds on stored tobacco and other dried vegetable products. Many other species attack a wide assortment of crops.

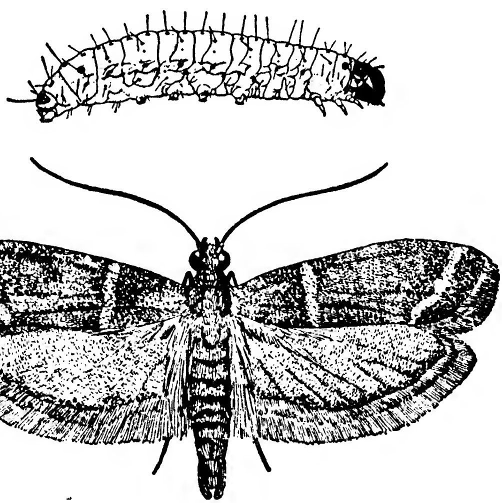

FIG. 347. The tobacco moth *Ephestia elutella,* larva and adult. (From U.S.D.A., B.E.P.Q.)

The "Macros"

In the Frenatae, most of the moth families containing the larger species, such as the miller moths, the various native "silkworm" moths, and the hawk moths, are usually referred to as the Macrofrenatae, or "macros." In these the hind wing usually is broad, has only a short fringe, and lacks vein 1*A*. As is the case with the "micros," the "macros" contain many families which are difficult for the non-specialist to identify.

Lasiocampidae. To this small family belong a few species of moderate size that have hairy larvae and velvety large-bodied adults. Tent caterpillars of the genus *Malacosoma,* fig. 348, are the best known of these. The larvae feed on a variety of deciduous trees, including

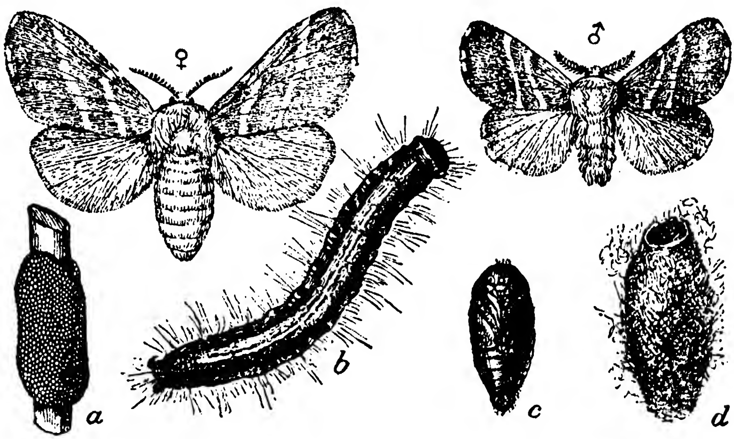

FIG. 348. Stages of the eastern tent caterpillar *Malacosoma americanum.* *a,* egg mass; *b,* larva; *c,* pupa; *d,* cocoon; ♀, female moth; ♂, male moth. (From U.S.D.A., B.E.P.Q.)

fruit trees, and periodically occur in outbreak numbers, the hordes of caterpillars defoliating thousands of acres of trees.

In the genus *Malacosoma,* winter is passed in the egg stage. The eggs hatch in late spring, and the young caterpillars of an egg mass spin a colonial webbed-nest, usually around the fork of a branch. The caterpillars leave this to feed on foliage, each individual returning via a silken thread left in its wake. The larvae leave the nest and pupate singly in a protected spot under bark or debris where the cocoons are constructed. Adults emerge in late summer, and, after mating, females deposit eggs in bands around small twigs. Each egg mass contains several hundred eggs, the whole incased in a secretion which hardens and becomes impervious to the elements.

During an outbreak year the adults may be attracted in huge numbers to the lights of towns. On a summer night in 1925 I witnessed a tremendous flight in Edmonton, Alberta. Throughout the entire business section the moths were about 6 inches deep, their greasy bodies completely stopping streetcar and automobile traffic, and making it difficult to walk. Under each street light and show window the moths formed piles reaching an apex from 2 to 3 feet high. The great majority died from suffocation by their fellows. Their rotting bodies gave a distinctive odor to the city streets for some time.

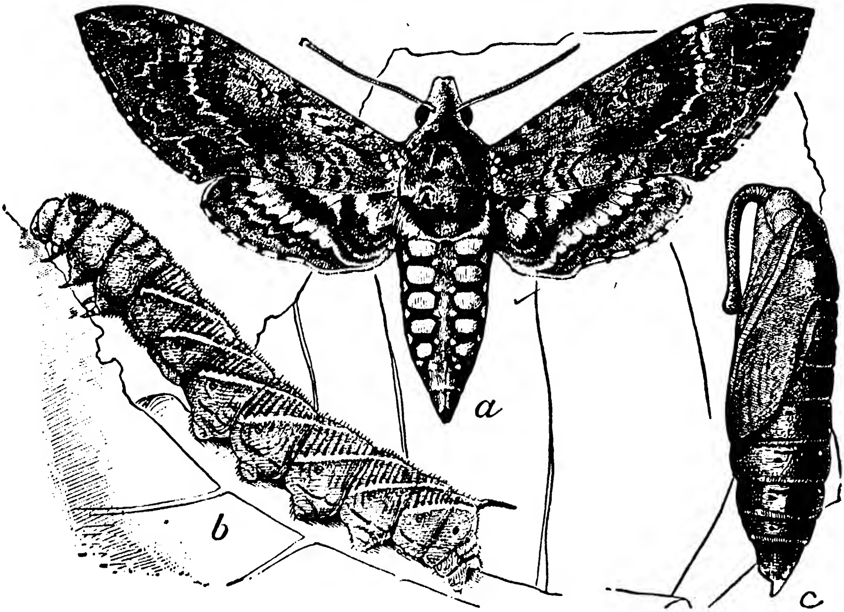

FIG. 349. A hornworm infesting tomato and tobacco, *Protoparce sexta*. *a*, adult; *b*, larva; *c*, pupa. (From U.S.D.A., B.E.P.Q.)

Sphingidae, Hawk or Sphinx Moths. These moths are all large, most of them having a wing spread of over 65 mm. (2½ inches). The body is stout and spindle-shaped, frequently tapering to a sharp point at the posterior end. When spread, the posterior margins of the hind wings are seldom back as far as the middle of the abdomen; the front wings are long and proportionately narrow. The antennae are long and simple, frequently slightly thickened towards the tip. The moths are extremely rapid fliers and feed on nectar. The larvae are leaf feeders; most forms have a sharp horn on the eighth abdominal segment and are commonly called hornworms. In the main our species feed on a wide variety of herbs, vines, and trees. A few are of economic importance, particularly the tomato hornworm *Protoparce quinquemaculata* and the tobacco hornworm *Protoparce sexta*, fig. 349.

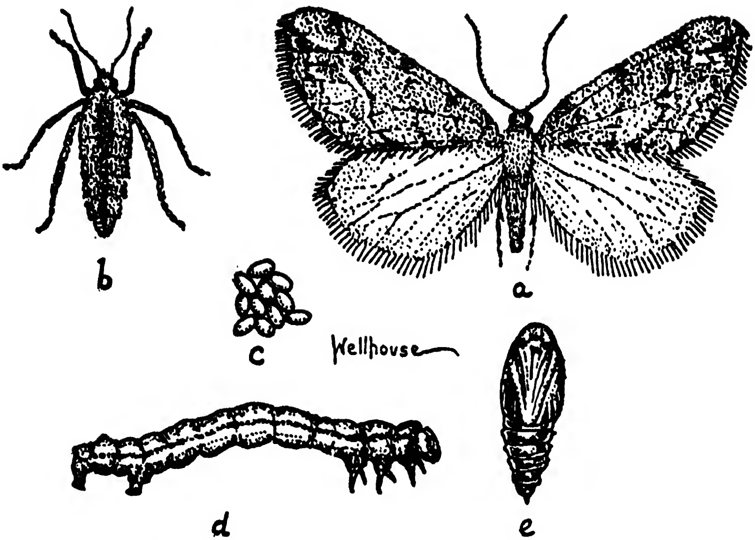

FIG. 350. The spring cankerworm *Paleacrita vernata*. *a*, male; *b*, female; *c*, eggs; *d*, larva; *e*, pupa. (From Wellhouse, "How Insects Live," by permission of The Macmillan Co.)

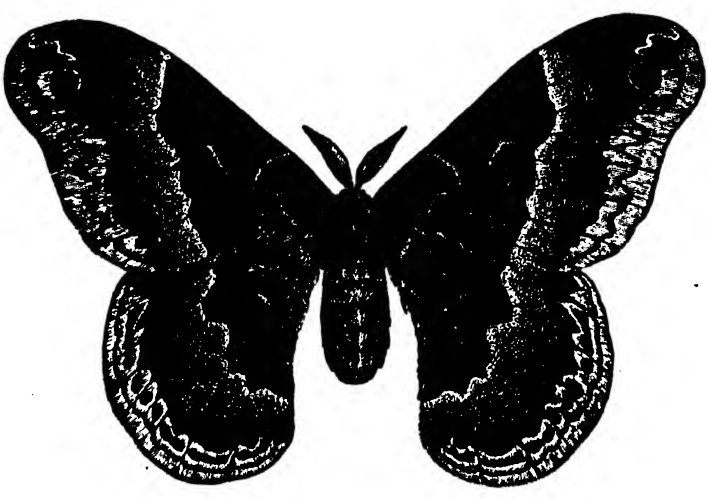

FIG. 351. The promethea moth *Callosamia promethea*. (From Comstock, "Introduction to Entomology," by permission of the Comstock Publishing Co.)

Geometridae, Measuring Worms, Geometers. These are fragile moths, with slender or pectinate antennae, large delicate wings, and slender bodies, fig. 350. The larvae are well known for their peculiar walking habit, consisting of a series of looping movements. They have long

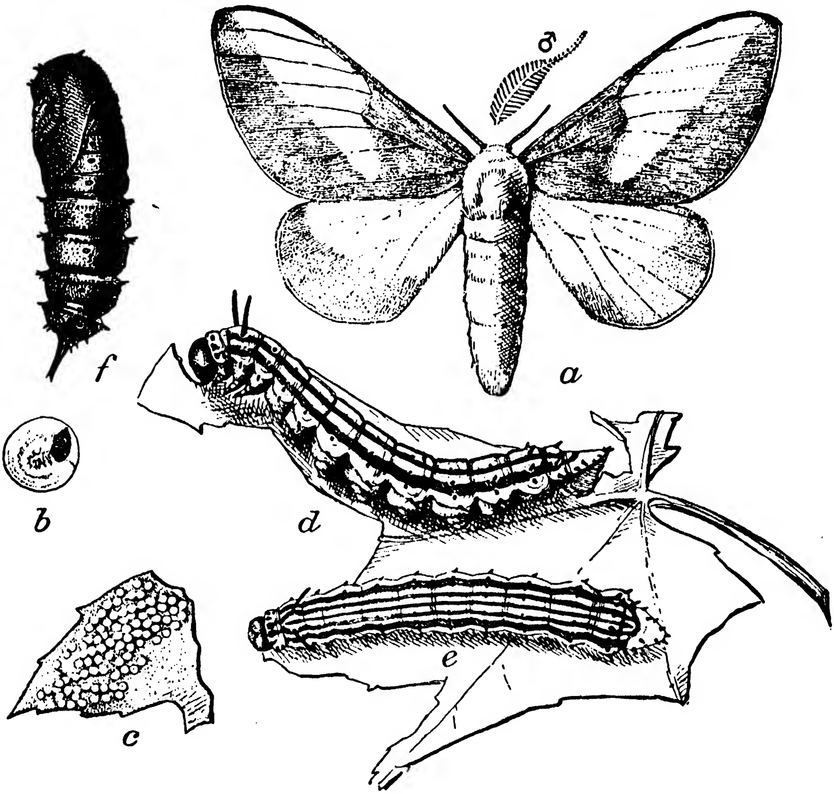

FIG. 352. The green-striped mapleworm *Anisota rubicunda*. *a*, female moth and antenna of male; *b*, egg showing embryo within; *c*, egg mass; *d*, *e*, larva; *f*, pupa. (From U.S.D.A., B.E.P.Q.)

slender bodies but only two or three pairs of large abdominal legs, located near the end of the body. When they are walking, the abdomen is raised in a high loop, and the hind legs are brought forward to grasp a supporting position close to the thoracic legs; these latter are then released, the body stretched forward, and a new grip taken by the thoracic legs at the end of the reach. The hind legs then let go, the body arches, and the operation is repeated. Geometers make up a large family; their host list includes many plant families and genera. Certain species are common defoliators of deciduous and coniferous trees. Some species, known as cankerworms, fig. 350, are locally very destructive to shade and fruit trees; these species have normal winged males but completely apterous females.

Saturniidae, Giant Silkworm Moths. Here belong the largest North American moths and caterpillars. The adults are velvety or woolly, with broad wings having a showy pattern. The hind wings have no trace of a frenulum; instead the basal portion of the anterior margin

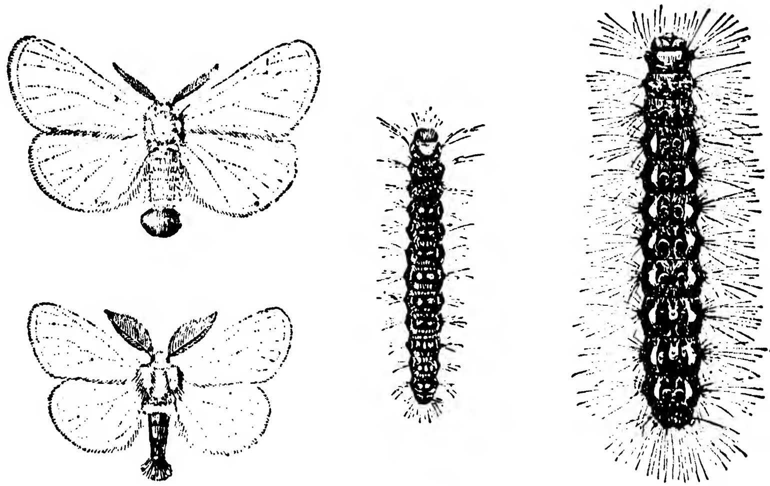

FIG. 353. The brown-tail moth *Nygmia phaeorrhoea;* female above, male below, larva in center, enlarged larva to right. (From U.S.D.A., B.E.P.Q.)

is enlarged and projects under the front wing in the flight position, thus synchronizing the two pairs. The antennae are feathery in the males and frequently in the females also. The caterpillars are leaf feeders; the larger ones have a voracious appetite and will consume an entire large leaf with astonishing speed. The larvae are stout bodied, bear spiny tubercles or tufts of stiff hairs, and may attain a length of 100 mm. (nearly 4 inches). The full-grown larvae spin large brown cocoons on branches or twigs near the ground, pupate, and pass the winter in this stage. A common eastern species is the promethea moth *Callosamia promethea,* fig. 351, which has a reddish or brown adult; the larva is green with yellow, red, and blue spiny tubercles.

The related family Citheroniidae contains the green-striped mapleworm *Anisota rubicunda,* fig. 352, a widespread species east of the Rocky Mountains.

Liparidae. This also is a small family containing species of only moderate size. The caterpillars are hairy, the adults frequently fuzzy. In several genera the females cannot fly, having only small padlike

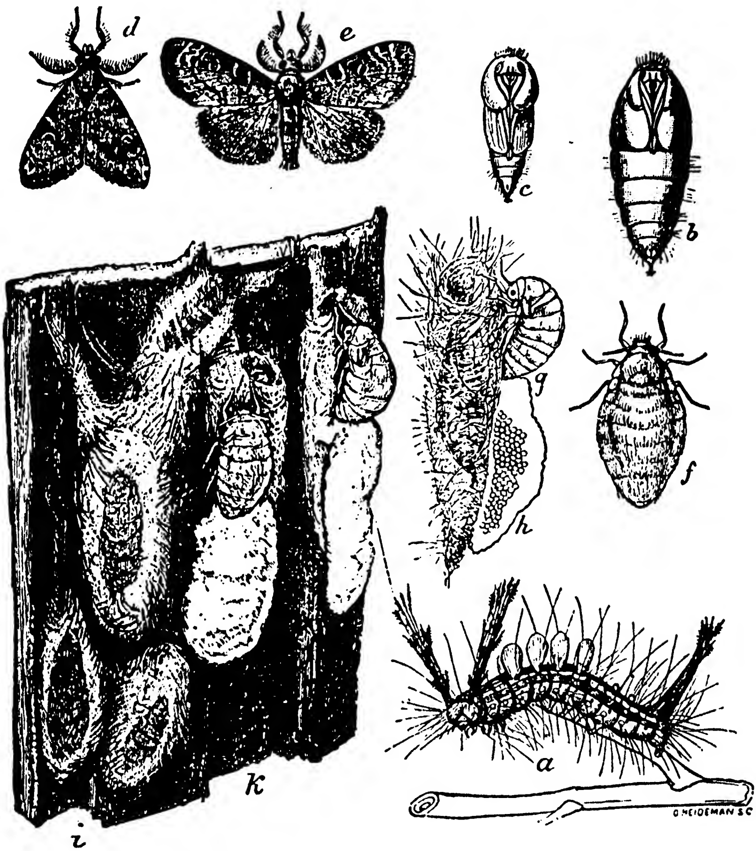

FIG. 354. The white-marked tussock moth *Hemerocampa leucosstigma.* *a,* larva; *b,* female pupa; *c,* male pupa; *d, e,* male moth; *f,* female moth; *g,* same ovipositing; *h,* egg mass; *i,* male cocoons; *k,* female cocoons, with moths laying eggs. (From U.S.D.A., B.E.P.Q.)

wings. To this family belong a few species of extreme economic importance, including the gypsy moth *Porthetria dispar* and the browntail moth *Nygmia phaeorrhoea,* fig. 353. Both these gained entrance to the United States from Europe and are destructive enemies of shade trees in northeastern United States. Another species of Liparidae attacking a wide variety of deciduous trees is the white-marked tussock moth *Hemerocampa leucostigma,* fig. 354. The tussock moth larvae has tufts of long nettling hairs at each end of the body, and "pencils" of white hairs on some of the central segments. It makes a cocoon on the bark of trees. The female is grublike; she lays a large group of eggs encased in a foamy white secretion that forms a protective covering for them.

Noctuidae, Owlet or Miller Moths. This is by far the largest family of the Lepidoptera. The adults vary greatly in size, shape, and color; the structural characters are also diverse, so that the family can be distinguished from its relatives only on the basis of a combination

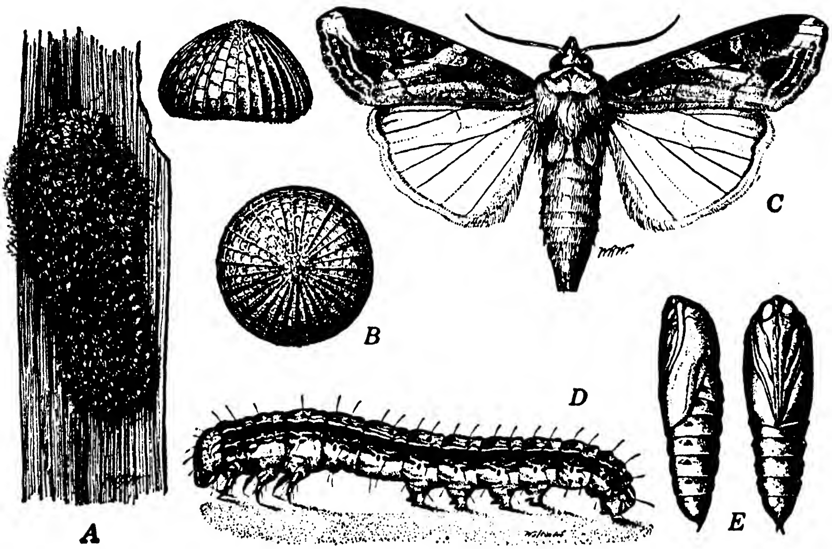

FIG. 355. The fall armyworm *Laphygma frugiperda.* *A,* egg mass; *B,* eggs; *C,* adult; *D,* larva; *E,* pupa. (From U.S.D.A., B.E.P.Q.)

of several critical differences. The larvae are usually leaf feeders or stem or root borers and for the most part are unadorned with horns or conspicuous processes. From the standpoint of agriculture the family is an important once. It includes many species whose larvae, called cutworms, attack a wide variety of grain, truck, and field crops. Other economic species are the armyworm *Cirphis unipuncta* and the fall armyworm *Laphygma frugiperda,* fig. 355, which attack pasture grasses, corn, and small grains; the corn earworm or cotton bollworm *Heliothis armigera,* fig. 356, which attacks cotton, corn, tomatoes, and other crops; and the cabbage looper *Trichoplusia ni,* fig. 357, which feeds on cruciferous crops and "loops" like a geometrid larva, but has only two middle pairs of abdominal legs. In all these the larvae do the damage.

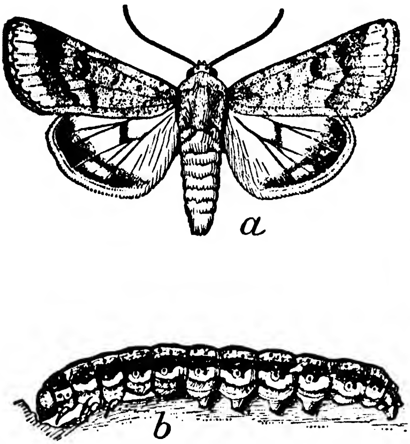

FIG. 356. The corn earworm or cotton bollworm *Heliothis armigera.* *a,* adult; *b,* larva. (From U.S.D.A., B.E.P.Q.)

FIG. 357. The cabbage looper *Trichoplusia ni.* *a,* adult; *b,* eggs; *c,* larva; *d,* pupa. (From U.S.D.A., B.E.P.Q.)

Arctiidae, the Arctiid Moths. This family is a close relative of the Noctuidae, differing from it mainly in that the adults are usually white or yellow or have intricate bright or yellow patterns. The larvae have thick tufts of hairs, and hence many of them are called woolly bears. These larvae are a common sight in late summer, hurrying along the ground looking for a sheltered place to make a cocoon and pupate.

Other Moths. There are many other moths, some of striking appearance, others similar in general characteristics to the few just mentioned. To identify these the student is referred to the works listed at the end of the section on Lepidoptera.

Suborder RHOPALOCERA

Butterflies and Skippers

In this suborder the hind wings have no frenulum, and in both front and hind wings the stem of media has been lost, resulting in a large central discal cell. Most of the species are brightly patterned. The adults are diurnal in habit and lovers of sunshine, in marked contrast to the crepuscular or nocturnal habit of most of the moths. When at rest, the Rhopalocera hold their wings upright over the body instead of folding them flat on the body as do the moths. The suborder is divided into two well-marked groups: the skippers and the butterflies.

Skippers. These are very rapid on the wing, able to fly in a straight line like a wasp or hawk moth. Most of our species belong to the Hesperiidae; they are dull colored, with yellow and brown predominating, and are less than 30 mm. from wing tip to wing tip. Except for a few species, the larva has a large head accentuated by a small necklike prothorax. Most of the species live in a nest made by sewing together a few leaves of the host plant. A common eastern species is the silver-spotted skipper *Epargyreus tityrus,* which feeds on several legumes; *Wisteria* is a favorite.

Butterflies. The inversion "flutterbys" is descriptive of the flight of most members of this group. They have a very slow rate of wing stroke and hence fly in a series of up-and-down movements producing an erratic course. The butterfly group is represented in North America by seven families, most of which have members well known to the naturalist.

Papilionidae, the Swallowtailed Butterflies. In this small family, fig. 358, the margin of the hind wing is usually notched, and the vein M_3 ends in a finger-like projection or tail. These are large butterflies, many of them gaudily spotted or striped with many colors, yellow predominating in several species. The larvae are leaf feeders and may be as conspicuously marked as the adults. They are unique in having a forked eversible stink gland, or *osmeterium,* fig. 358*b,* on the dorsum of the pronotum. This is shot out when the larva is alarmed; it is usually bright orange and emits a pronounced odor.

Pieridae, the Whites and Sulphurs. These are predominantly white, yellow, or orange butterflies, some with extensive black markings. The larvae have an abundant supply of stiff hairs and look bristly. The imported cabbageworm *Pieris rapae,* fig. 359, whose adult is white marked with black dots, occurs commonly in the central and northern states. The larvae are green and are pests of cabbage and related plants. This is an introduced species from Europe. A native species of the same genus, *P. protodice* the southern cabbageworm, is a pest

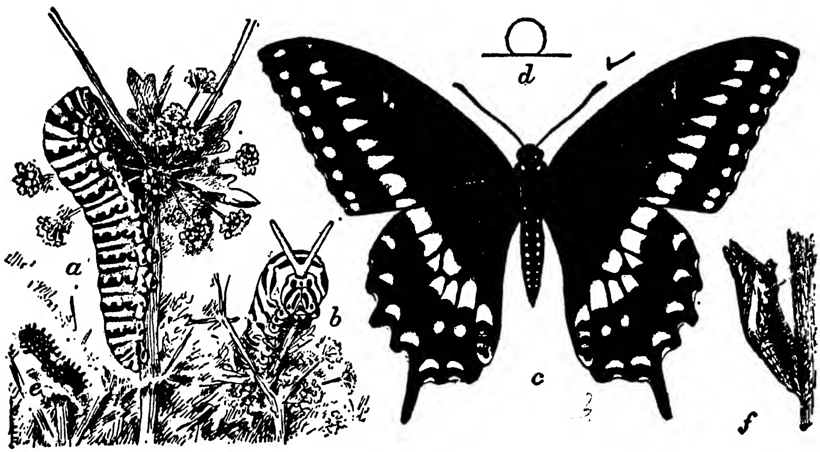

FIG. 358. The celery swallowtail *Papilio polyxenes*. *a*, larva from side; *b*, larva showing head with odoriferous appendages; *c*, male butterfly; *d*, outline of egg; *e*, young larva; *f*, chrysalis. (From U.S.D.A., B.E.P.Q.)

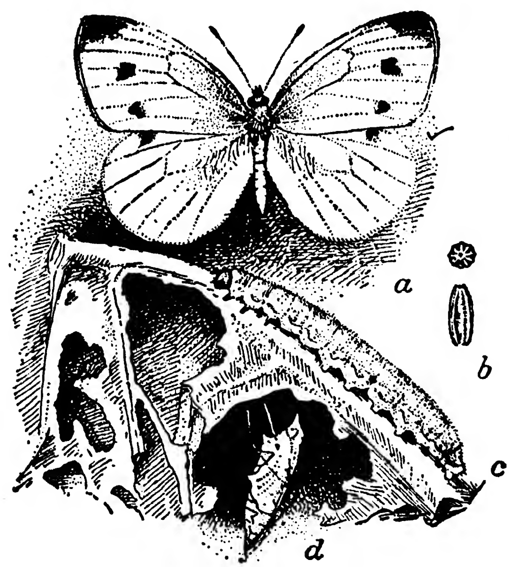

FIG. 359. The imported cabbageworm *Pieris rapae*. *a*, female butterfly; *b*, egg (above as seen from above, below as seen from side); *c*, larva, or worm, in natural position on cabbage leaf; *d*, suspended chrysalis. (From U.S.D.A., B.E.P.Q.)

of cruciferous crops in the southern states. Another pierid that is often a pest locally is *Colias philodice eurytheme* the alfalfa butterfly or orange sulphur. It is a highly variable species in color and occurs over most of the continent. The larva feeds on alfalfa, clover, and certain other legumes.

Other Butterflies. In North America there are many species of butterflies in addition to the few just listed. Every locality on the continent has a selection from strikingly colored to somber forms, many of them abundant locally. For more information regarding their identification characters, hosts, and range, the student is referred to Dr. Holland's "Butterfly Book," listed among the following references.

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Order DIPTERA

Flies

Typical adults, fig. 360, have a single (front) pair of membranous wings, rarely scaled. The wings have few crossveins and a moderate number of veins. The hind wings are represented only by a pair of slender knobbed balancing organs, called *halteres*. Mouthparts are of various types; in some groups they are modified for piercing and sucking, in other groups for rasping and lapping. The body form is diverse. In a few groups the adults are completely apterous. The eyes are usually large; the antennae vary from 3- to 40-segmented. These are holometabolous insects with legless larvae, usually either with a distinct mandibulate head, fig. 367, or with an internal sclerotized skeleton attached to a pair of hooklike mandibles. The pupae are either free or are formed within the last larval skin.

The order Diptera is a large one, including over fifteen thousand North American species. The food and habitat of the adults are usually very different from those of the larvae.

Adults of many families feed chiefly on nectar and plant sap or on free liquids associated with rotting organic matter. Certain groups, such as mosquitoes and horseflies, feed on animal blood; these have mouthparts highly modified for piercing and sucking. In a few groups, for example, the bot flies, the mouthparts are so vestigial that it is doubtful if the adults take any nourishment.

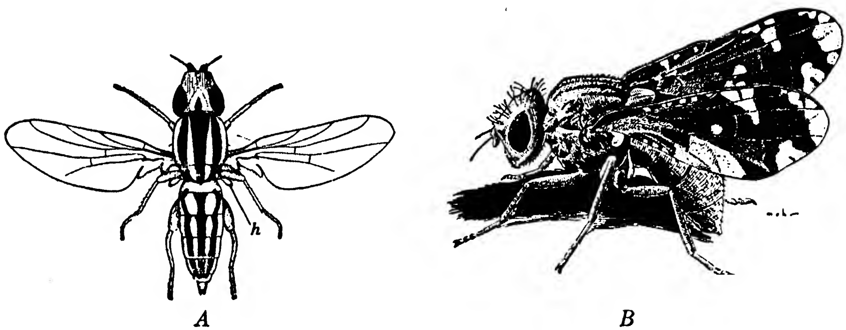


FIG. 360. Typical flies. *A, Meromyza america; B, Trypeta solidaginis; h,* haltere. (From Illinois Natural History Survey)

As a group, fly larvae are moisture-loving, the great majority living in water, in rotting flesh, inside the bodies of other animals, in decaying fruit or other moist organic material, or inside living plant tissue. A few live in relatively dry soil or move about exposed to the air, but these are the exceptions rather than the rule.

For the most part, fly eggs are simple, ovoid or elongate, and are normally laid singly, in, on, or near the larval food. Some, such as those of *Drosophila,* have lateral or polar floats which prevent them from sinking into semiliquid food and drowning. Eggs of certain mosquitoes are sufficiently well protected against the elements to withstand months of alternate drying, wetting, and freezing. In some groups, such as the flesh flies and some parasitic flies, the eggs may hatch just before leaving the body of the female and are deposited as minute larvae. This habit is carried to extreme development in the sheeptick groups (Pupipara) where the larvae hatch and grow to their full size in the body of the female. Of unusual interest in the order is the pedogenesis exhibited by some species of midges (see p. 203).

The Diptera comprise three well-marked groups or suborders, the Nematocera, Brachycera, and Cyclorrapha.

Synopsis of Suborders

1. Larval mandibles working in a horizontal plane, and usually having teeth or brushes used in gathering or grasping food. Adult antennae composed of at least 7 segments which are not fused into a solid structure...... **Nematocera**
   Larval mandibles hooklike or knifelike and working in a vertical (up-and-down) plane. Adult antennae either with less than 7 segments or having the segments of the flagellum fused into a solid structure, usually surmounted by a dorsal or terminal style or arista.......................................2
2. Either pupa free, not inclosed in last larval skin, or the adult escaping from puparium by means of a dorsal slit. Adults without a ptilinum or frontal lunule ....**Brachycera**
   Pupa always inclosed in last larval skin, which forms a puparium; adult usually escapes from puparium by pushing off the anterior end, which then looks like a round cap. Adults usually having a ptilinum or frontal lunule **Cyclorrapha**

Key to Common Families

1. Abdomen only indistinctly segmented; the coxae of the 2 legs of each segment far apart. Adults living as parasites on birds or mammals...............2
   Abdomen having distinct segments; the 2 legs of each segment held fairly closely together, sometimes the coxae almost contiguous. Not living as ectoparasites in the adult stage......................................3
2. Palpi long and slender, forming a sheath for the mouthparts. Living on birds and mammals with the exception of bats............**Hippoboscidae, p. 421**
   Palpi broader than long, not incasing the mouthparts. Parasitic on bats **Streblidae**
3. Antenna having more than 3 segments, fig. 363*F*, *G*, *H*, not counting a style or arista, borne by the third.......................................4
   Antenna having 3 segments or less; usually the third bears a style, fig. 363*O*, or arista, fig. 363*I*, *J*...19
4. Small mothlike flies, never longer than 5 mm., having body and wings densely clothed with hair or scales; wings having about 10 longitudinal veins, and having crossveins only at extreme base, fig. 361*A*............**Psychodidae**
   Appearance not mothlike, or venation of a different type..................5
5. Mesonotum having a distinct, V-shaped praescutal suture, fig. 363*A*; elongate species having long legs, fig. 364........................**Tipulidae, p. 404**
   Mesonotum with praescutal suture transverse, indistinct, or atrophied, fig. 363*B*, *C*...6
6. Antenna having 6 or more well-marked ringlike or beadlike segments, fig. 363*F* 7
   Antenna having only 4 or 5 segments, fig. 363*G*, or the terminal segment sometimes indistinctly subdivided, fig. 363*H*..............................15
7. Wing having cell Cu_{1b} either open at apex, fig. 361*E*, or lost due to atrophy of veins, 361*C* 8

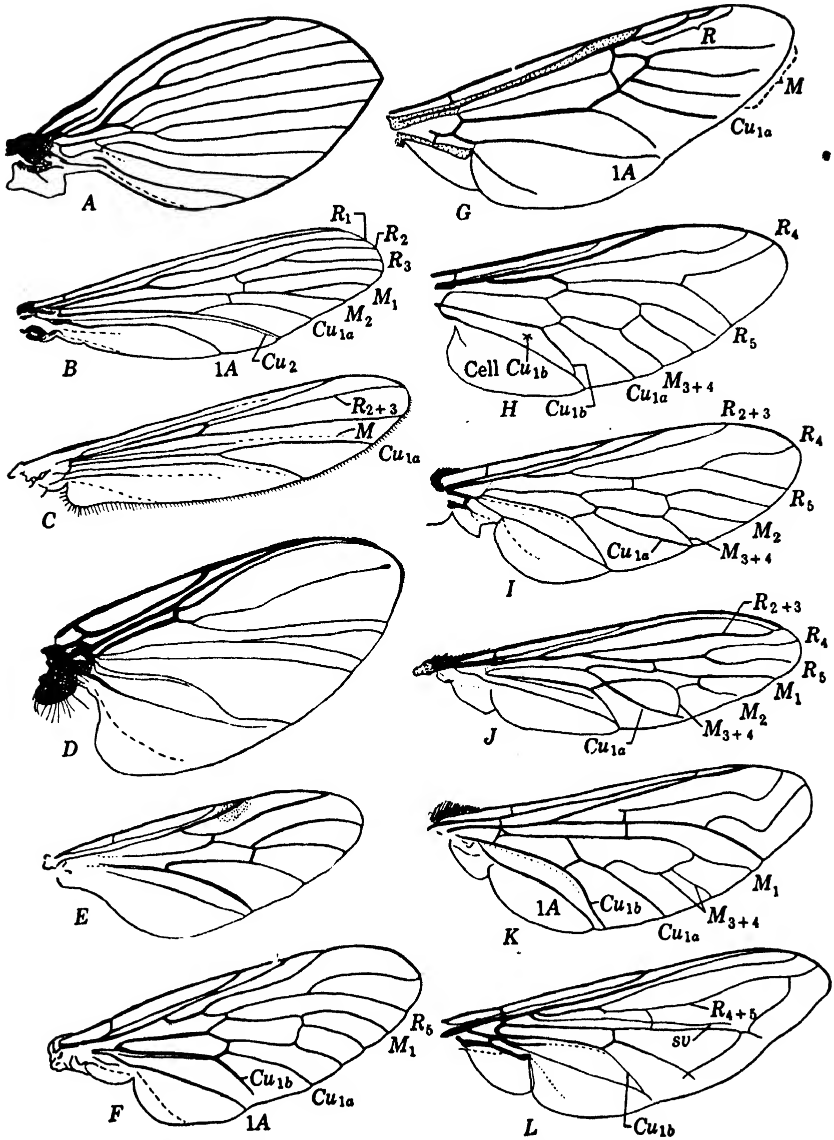


FIG. 361. Wings of Diptera. *A*, *Psychoda*, Psychodidae; *B*, *Aedes*, Culicidae; *C*, *Chironomus*, Chironomidae; *D*, *Simulium*, Simuliidae; *E*, *Bibio*, Bibionidae; *F*, *Rhagio*, Rhagionidae; *G*, *Stratiomys*, Stratiomyiidae; *H*, *Tabanus*, Tabanidae; *I*, *Thereva*, Therevidae; *J*, *Asilus*, Asilidae; *K*, *Anthrax*, Bombyliidae; *L*, *Scaeva*, Syrphidae; *sv*, spurious vein.

Wing having cell Cu_{1b} entirely closed at apex by fusion of veins Cu_{1b} and $1A$, fig. 361*I*....15

8. Wing having both R_{2+3} and M_{1+2} branched, and the venation fairly parallel, fig. 361*B*; mouthparts often forming a long slender beak, fig. 367 **Culicidae, p. 406**

Wing having either R_{2+3} or M_{1+2} unbranched, the venation frequently markedly divergent, fig. 361*E*; mouthparts never forming a long beak....9

9. Ocelli present....10

Ocelli absent....12

10. Anterior margin of wing only slightly more heavily sclerotized than apical and posterior margins....**Cecidomyiidae, p. 409**

Anterior margin of wing having a sclerotized thickening that stops abruptly at or just beyond juncture with R_{4+5}, fig. 361*D, E*....11

11. Antennae inserted below level of eyes, fig. 363*K, L*; front femur often enlarged **Bibionidae**

Antennae inserted on a level with middle of eyes; coxae often greatly elongated ....**Mycetophilidae**

12. Wing having 2 or 3 strong parallel veins near anterior margin and a group of 6 or 8 oblique very weak veins running from anterior region to or near posterior margin of wing, fig. 361*D*, antennae short, 12-segmented, the last 10 annular and closely knit, fig. 368....**Simuliidae, p. 408**

Wing having a different venation, either more veins equally sclerotized, or most of them longitudinal in general course rather than oblique, fig. 361*C*; antennae usually elongate, with well-separated segments....13

13. Anterior margin of wing only slightly more heavily sclerotized than apical and posterior margins....**Cecidomyiidae, p. 409**

Anterior margin of wing having a sclerotized thickening that stops abruptly at or just beyond juncture with R_{4+5}, fig. 361*C*....14

14. Postnotum very large, projecting some distance posterior to scutellum, fig. 363*C*; slender elongate flies....**Chironomidae, p. 405**

Postnotum smaller, scarcely projecting at all from beneath the scutellum, fig. 363*B*; small stouter flies....**Ceratopogonidae**

15. Tarsus having 3 whitish pulvillar pads, fig. 363*D*; the middle one (the empodium) is sometimes dorsad of the lateral pulvilli, which are sometimes small 16

Tarsus at most having 2 pulvillar pads, the empodium reduced to a seta, fig. 363*E*; the 2 pulvilli may be reduced, in which case the tarsus lacks pads...17

16. Wing with branches of R_s close to front margin, forming a group of narrow cells along it, fig. 361*G*; tibia without apical spurs....**Stratiomyiidae**

Wing with branches of R_s not crowded to front margin, R_4 and R_5 diverging to form a triangular cell embracing apex of wing, fig 361*H* **Tabanidae, p. 411**

17. Antenna having third segment elongate, fourth clavate, without arista or style, fig. 363*G*; very large species....**Mydaidae, p. 413**

Antenna having apical segment not clavate....18

18. Top of head sunken to form a deep excavation between eyes, fig. 363*M*; wing with M_2 present and M_{3+4} having its base almost or entirely free from Cu_{1a}, the latter 2 veins sometimes fused for a short distance at base and/or apex, fig. 361*J*....**Asilidae, p. 412**

Top of head without a deep excavation; wing having M_2 atrophied, and M_{3+4} fused near base for a considerable distance with Cu_{1a}, fig. 361*K* **Bombyliidae**

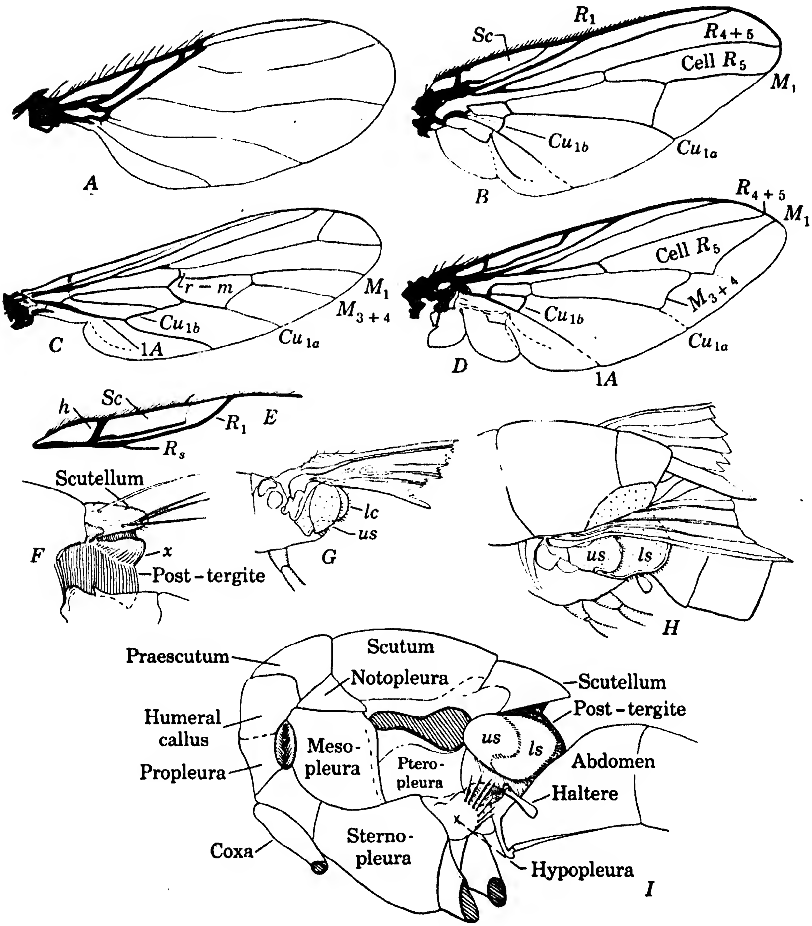


FIG. 362. Diagnostic parts of Diptera. *A*, wing of *Megaselia*, Phoridae; *B*, wing of *Hylemya*, Anthomyiidae; *C*, wing of *Empis*, Empididae; *D*, wing of *Sarcophaga*, Sarcophagidae; *E*, costal region of *Rhagoletis*, Tephritidae; *F*, scutellum of *Zenillia*, Tachinidae; *G*, squamae of *Anthomyia*, Anthomyiidae; *H*, squamae of *Musca*, Muscidae; *I*, thorax, diagrammatic, of higher Diptera. *ls*, lower squama; *us*, upper squama; *x*, secondary convexity on scutellum.

19. Wing at most having *Sc* and stem of *R* sclerotized, remaining venation consisting of 3 or 4 weak veins arranged as in fig. 362*A*; antenna composed of 1 segment and its arista . . . . **Phoridae**

Wing having a more extensive venation, figs. 362*B, C, D*; antenna may have 1 to 3 segments 20

20. Tarsus having 3 pulvillar pads, fig. 363*D*, 2 lateral and 1 mesal 21
Tarsus having only 2 (lateral) pulvillar pads, fig. 363*E*, or none 22

21. Antenna having distinct but faint annular lines on third segment, fig. 363*I*; wing having R_s and its branches forming a series of narrow cells along anterior margin, fig. 361*G* .... **Stratiomyiidae**
Antenna without annulations on third segment; wing having some branches of R_s ending at or below apex of wing, fig. 361*F* .... **Rhagionidae**

22. Wing having R_s with 3 branches, fig. 361*I, J* 23
Wing having R_s with only 1 or 2 branches, fig. 362*B, D* 26

23. Top of head sunken to form a deep excavation between eyes, fig. 363*M* **Asilidae**, p. 412
Top of head flat or convex, confluent in outline with top of eyes 24

24. Wing having M_{3+4} not fused at base with Cu_{1a} but frequently fusing with Cu_{1a} near margin; M_2 present, fig. 361*I*. Moderate-sized species similar to Asilidae in habits .... **Therevidae**
Wing having M_2 atrophied and M_{3+4} fused at base with Cu_{1a}, fig. 361K 25

25. Wing having Cu_{1b} reaching wing margin or fusing with 1*A* near wing margin. fig. 361*K* .... **Bombyliidae**
Wing having Cu_{1b} fused with 1*A* considerably before wing margin, fig. 362*C* **Empididae**

26. Wing with Cu_{1b} straight and long, angled only slightly from stem of *Cu*, fig. 361*L*; wing usually having a veinlike thickening, or "spurious vein," between R_s and *M* .... **Syrphidae**, p. 413
Wing with Cu_{1b} markedly angled from its parent vein, appearing like a cross-vein, fig. 362*B*; spurious vein never developed 27

27. Lower squamae large and platelike, upper squamae frequently large, but never more than half as long as lower ones, fig. 362*H, I* 28
Lower squamae short, often appearing as a thin band along body wall, upper squamae never long but frequently as long as lower ones, fig. 362*G* 33

28. Oral opening either a minute circle or a small triangular cleft, as in fig. 363*P*; body fuzzy with long dense hair .... **Oestridae**, p. 420
Oral opening large, fig. 363*Q*; body usually not fuzzy but often spiny in appearance 29

29. Hypopleura with only weak scattered hairs or none .... **Muscidae**, p. 418
Hypopleura with a row of bristles, fig. 362*I* 30

30. Wing having cell R_5 narrowed, with only a small apical opening, fig. 362*D* .. 31
Wing having cell R_5 only slightly narrowed at apex, as in 362*B* **Muscidae**, p. 418

31. Mesopostnotum having a convex bump below the scutellum, fig. 362*F* **Tachinidae**, p. 420
Mesopostnotum having no well-developed extra bump, at most a gentle convexity below scutellum 32

32. Arista of antenna with feathering not extending much beyond middle; body dull black or striped with gray and black .... **Sarcophagidae**
Arista feathered to tip, fig. 363*J*, or body entirely metallic blue or green **Calliphoridae**

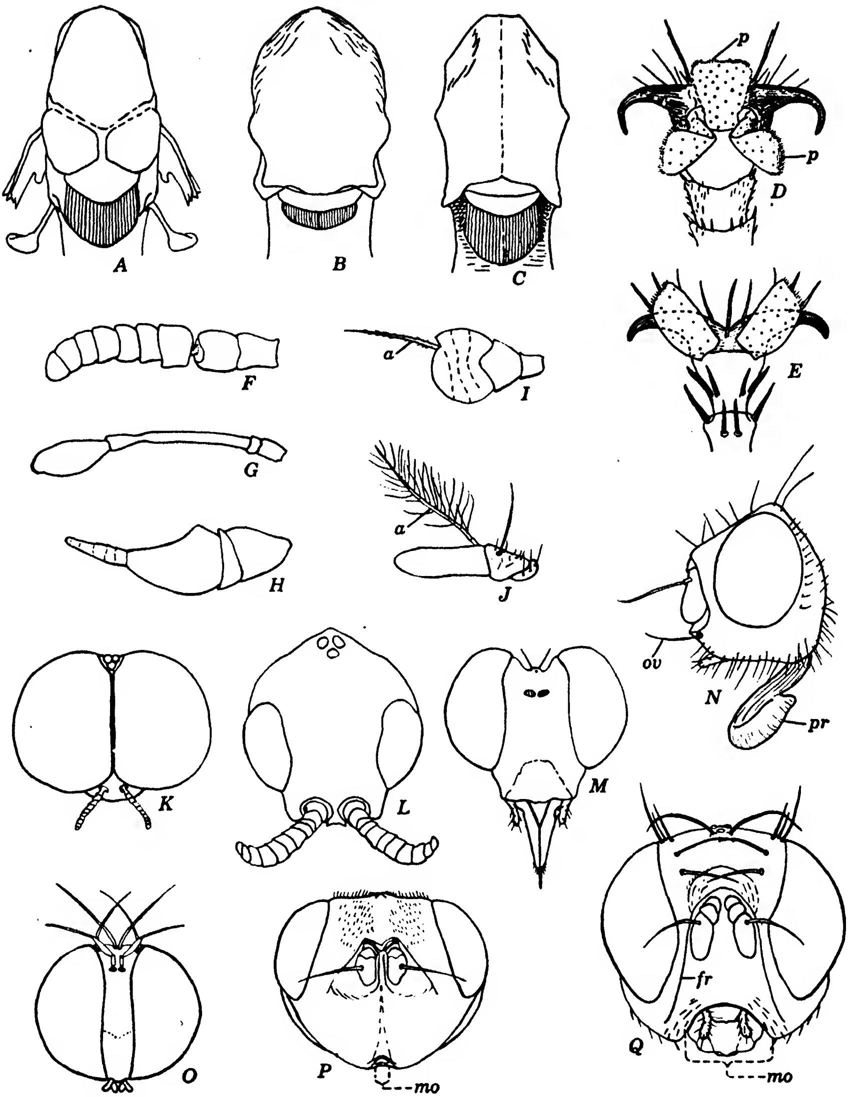


Fig. 363. Diagnostic parts of Diptera. *A*, mesonotum of *Helobia*, Tipulidae; *B*, mesonotum of *Palpomyia*, Ceratopogonidae; *C*, mesonotum of *Chironomus*, Chironomidae; *D*, tarsal claws and pads of *Tabanus*, Tabanidae; *E*, tarsal claws and pads of *Zenillia*, Tachinidae; *F*, antenna of *Bibio*, Bibionidae; *G*, antenna of *Mydas*, Mydaidae; *H*, antenna of *Tabanus*, Tabanidae; *I*, antenna of *Geosargus*, Stratiomyiidae; *J*, antenna of *Pollenia*, Sarcophagidae; *K* and *L*, face of *Bibio*, Bibionidae, male and female; *M*, face of *Asilus*, Asilidae; *N*, head of *Hylemya*, Anthomyiidae; *O*, face of *Dolichopus*, Dolichopodidae; *P*, face of *Gasterophilus*, Gasterophilidae; *Q*, *Tephrita*, Tephritidae. *a*, arista; *fr*, frontal ridge or suture; *mo*, mouth opening; *ov*, oral vibrissa; *p*, pulvillar pads; *pr*, proboscis.

33. Oral opening round and minute, mouthparts vestigial, cheeks inflated, fig. 363*P* **Gasterophilidae,** p. 416
Oral opening large, mouthparts well developed 34
34. Front of head lacking sutures or ridges running ventrolaterad from base of antennae, fig. 363*O* 35
Front of head having a pair of frontal sutures or ridges, *fr*, each running from near the antenna to the oral excavation, fig. 363*Q* 36
35. Crossvein *r-m* situated at the base of the wing, and inconspicuous, sometimes difficult to find; free end of M_{3+4} lacking .... **Dolichopodidae**
Either crossvein *r-m* situated at least one-third distance from base to apex of wing, or M_3 present, fig. 362*C* .... **Empididae**
36. *Sc* strong for its entire length, curving gently to join *C* before R_1 does, fig. 362*B* (this character best seen from anterodorsal view of wing) 37
Sc either partially atrophied, or fused at tip with R_1, or abruptly angled, fig. 362*E* 38
37. Oral vibrissae present, fig. 363*N*; wings usually plain .... **Anthomyiidae,** p. 418
Oral vibrissae absent; wings of many species brightly patterned ...... **Otitidae**
38. Wing having costal cell wide and having *Sc* ending abruptly or angled abruptly much before apex of cell, either *Sc* beyond this point weak or atrophied, or *C* with a distinct break, at which point there are several stout bristles, fig. 362*E* **Tephritidae,** p. 415
Wing either having costal cell narrow, or *Sc* gradually fading out towards its apex, or fusing with R_1. Several families of small flies difficult to identify as to family, including .... **Drosophilidae,** p. 416, **Ephydridae,** and **Chloropidae.**

Suborder NEMATOCERA

The North American fauna contains representatives of about twenty families of Nematocera. Midges, craneflies, mosquitoes, and blackflies are examples of the more abundant and conspicuous families. The larvae of most families have a well-defined sclerotized head, fig. 366, retracted into the thorax only in the Tipulidae.

Tipulidae, Craneflies. The adults are long-legged slender-winged flies, fig. 364; the antennae are threadlike, with many distinct segments, and the mesonotum has a V-shaped transverse furrow or suture. The adults are extremely abundant in moist woods and sheltered ravines, and along wooded stream banks. The larvae are elongate and wormlike, fig. 365; many are aquatic, living especially in submerged clusters of rotting leaves; many feed in leaf mold; and a few feed on living plant roots or mine in leaves. They vary greatly in size and appearance but have in common a stout head which is partly retracted within the thorax (in certain species it is further retractile and may be completely hidden in the thorax when the insect is disturbed) and strong toothed mandibles which work from side to side.

Chironomidae, Midges. These are frail insects, fig. 366, frequently mistaken for mosquitoes, but they do not bite and have several structural differences which set them off. The male antennae are plumose with whorls of long silky hair. The larvae are all aquatic, some free

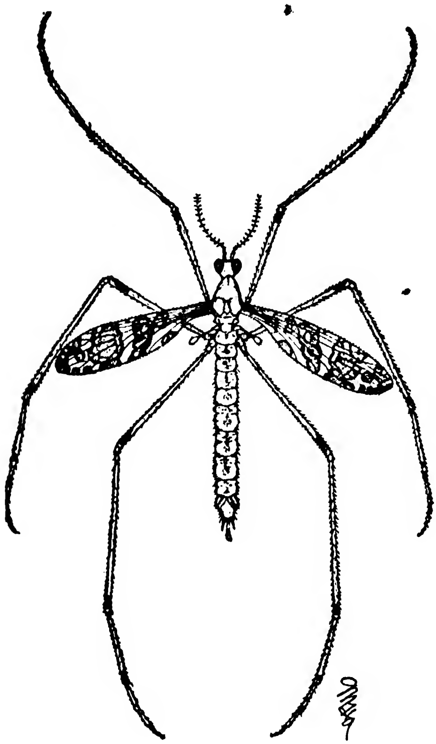


Fig. 364. A cranefly *Epiphragma fascipennis*, adult female.

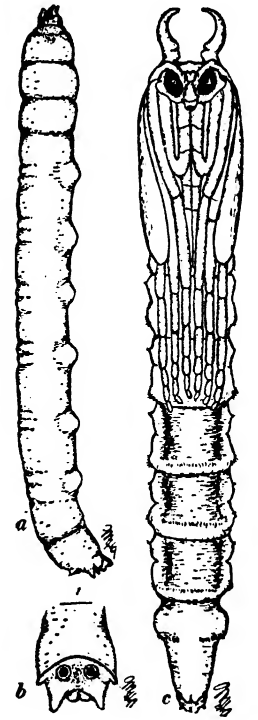


Fig. 365. *Epiphragma.* *a*, larva; *b*, end of larva from above; *c*, pupa. (After Needham)

living, others spinning a loose web of bottom particles and silk and in certain genera making a definite case. They are slender and wormlike, with a small but distinct sclerotized head, and a 12-segmented body. In some groups the prothorax, or the last body segment, or both, may have a pair of non-jointed leglike protuberances or pseudopods. The larvae feed on organic matter on the bottom of bodies of water and are found in rivers, lakes, ditches, and stagnant ponds. The pupae are also aquatic, some of them free living, but most of them staying in the web or case made by the larva. In many bodies of water these midge larvae are tremendously abundant and form one of the principal items of fish food. When the adults emerge, they appear in clouds and at night blanket near-by lights in a humming mass. The eggs are laid in water and hatch in a few days.

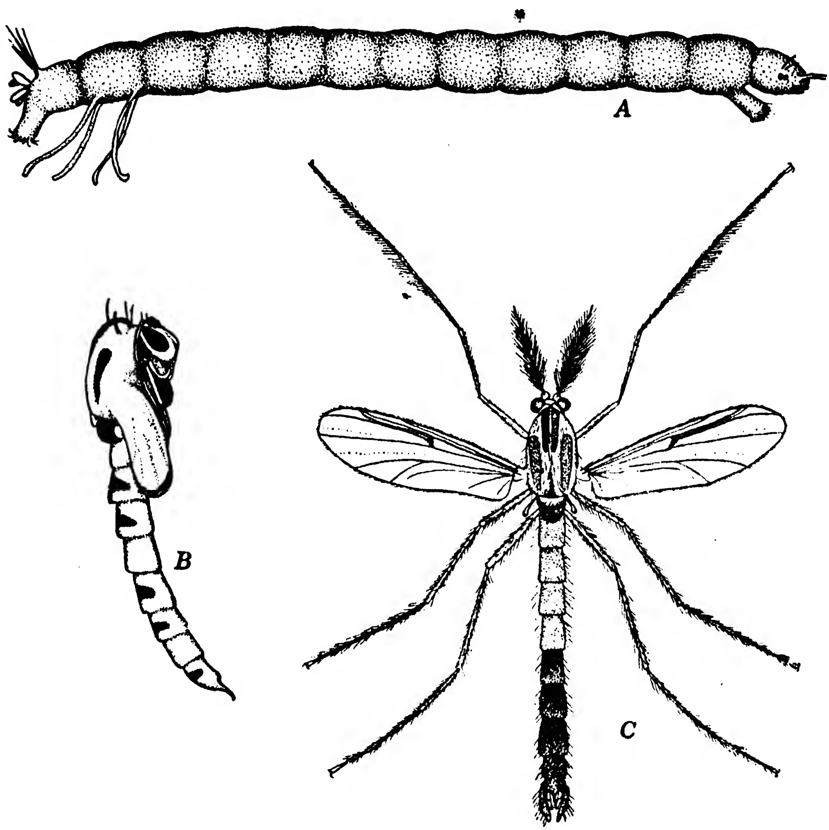


FIG. 366. Life history stages of Chironomidae. *A*, larva of *Chironomus tentans*; *B*, pupa of *Cricotopus trifasciatus*; *C*, adult male of *Chironomus ferrugineovittatus*. (From Illinois Natural History Survey)

Culicidae, Mosquitoes, Fig. 367. Long-legged slender insects, having beadlike antennae (in the males they are plumose as in the Chironomidae) and many-veined wings. One small subfamily, the Chaoborinae (non-biting mosquitoes), have mouthparts that resemble pads. All the true mosquitoes belong to the subfamily Culicinae. In these the mouthparts form a beak, composed of a highly modified assemblage of piercing-sucking parts (see fig. 77, p. 78).

In certain genera eggs are laid on water, either singly or glued together to form rafts; they hatch in a few days. In other genera eggs

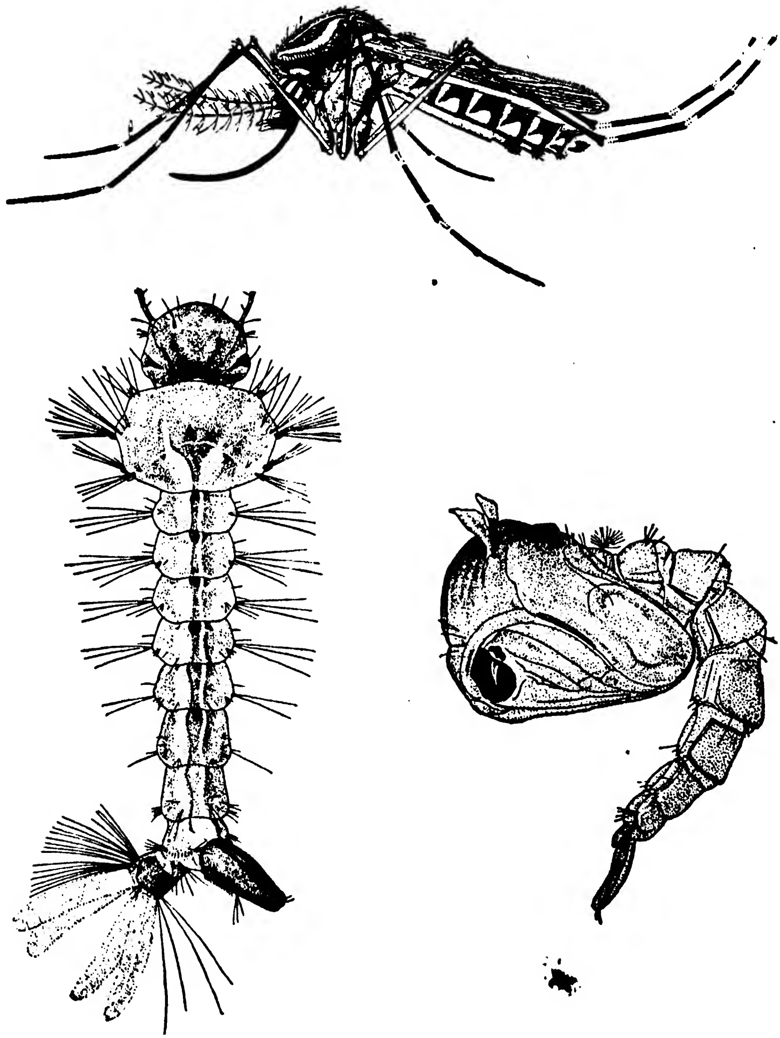


FIG. 367. The yellow fever mosquito *Aedes aegypti*. Adult above; larva at left; pupa at right. (From U.S.D.A., B.E.P.Q.)

are laid in humus or just above the water line on the sides of containers; these eggs hatch at some later time when the water rises and inundates them. The larvae are aquatic, most of them living in still water, but a few species live in slowly moving water. In other parts of the world there are species which breed in rapid streams, quite in contrast with the habits of nearctic species. The larvae are called wrigglers; they have large heads with fairly long antennae, a large swollen thorax, and a cylindrical abdomen. In all the true mosquitoes and certain of the others the abdomen bears a dorsal breathing tube or plate on the eighth segment. In the main, mosquito larvae feed on microorganisms and organic matter in or on the water. A few groups are predaceous and feed solely on other mosquito larvae. The pupae, which are called tumblers, are also aquatic, free living, and active. Their breathing tubes are situated on the thorax. Adult females of a few species and males of all mosquito species feed only on nectar or water. But unfortunately in most species the females seek a blood meal, which in their case is necessary for reproduction.

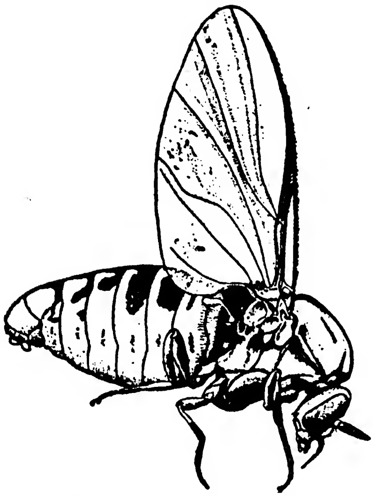


FIG. 368. Adult blackfly *Simulium vittatum*. (After Knowlton and Rowe)

Economically, mosquitoes are of tremendous importance to man. Some species, principally those of the genera *Anopheles* and *Aedes*, transmit an imposing list of human diseases, including malaria, dengue, yellow fever, and filariasis. For this reason mosquitoes are of utmost importance in a consideration of medical entomology. As a direct nuisance mosquitoes have an economic influence. The severity of their attacks decreases property values, especially in resort areas, and has undoubtedly had an influence in the settlement of extreme northern areas where mosquitoes are unusually abundant.

Simuliidae, Blackflies. This family, often referred to as buffalo gnats, has aquatic larvae and pupae and bloodsucking adults, like the Culicidae. The blackflies are short, stubby, and humpbacked, with short legs and compact 11-segmented antennae, fig. 368. Unlike the mosquitoes, both sexes bite. Horses, cattle, ducks, and many wild animals are attacked. Certain species attack man also, gathering around the ears, eyes, and exposed areas of the face, hands, and ankles. They draw a great amount of blood and produce burning welts on the victim's skin. These welts may itch and burn for a week or more.

The eggs are laid in clusters near the water edge or in the water. The larvae are sedentary, elongate, and slightly vasiform, fig. 369, and occur only in running water; the posterior end is anchored by a hooked sucker–disc to some support such as a rock, log, or trailing leaves; the head has a pair of feathery branched rakes which are supposedly used

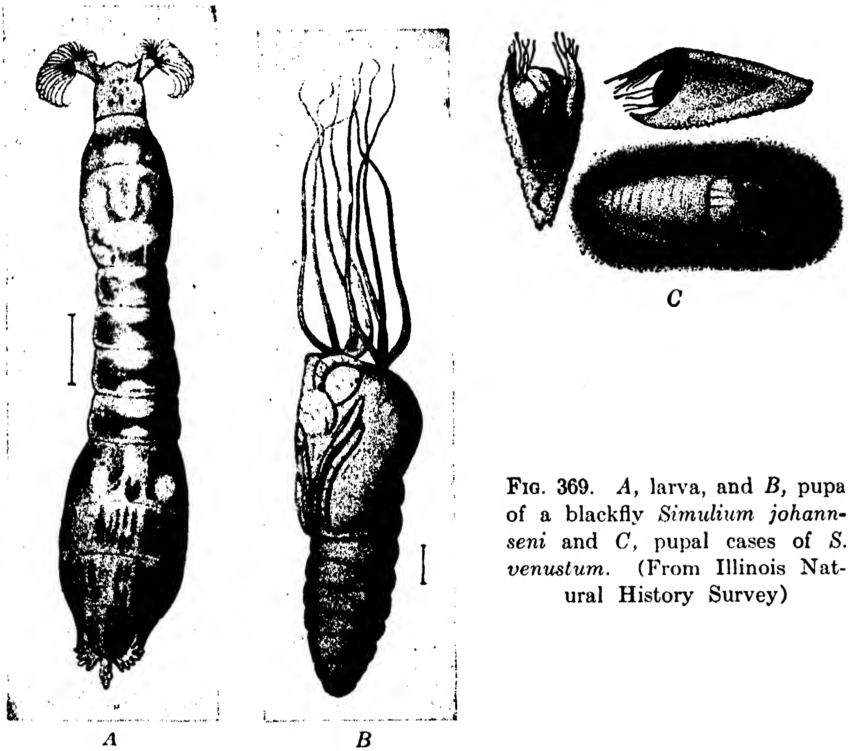


FIG. 369. *A*, larva, and *B*, pupa of a blackfly *Simulium johannseni* and *C*, pupal cases of *S. venustum*. (From Illinois Natural History Survey)

as strainers to obtain food from the running water, primarily microorganisms and organic material. The pupae are also aquatic, formed in a boot-shaped cocoon, fig. 369. On the prothorax of the pupa are a pair of long respiratory processes, usually branching into many slender filaments.

Cecidomyiidae, the Gall Gnats, Fig. 370. The adults are inconspicuous fragile flies, having greatly reduced wing venation, and elongate beadlike antennae. The adults feed only on aqueous material such as sap; the larval period of the life cycle is the part in which most of the food is consumed. There are many genera of the gall makers, and it is by these galls, especially on willows, deciduous trees, and

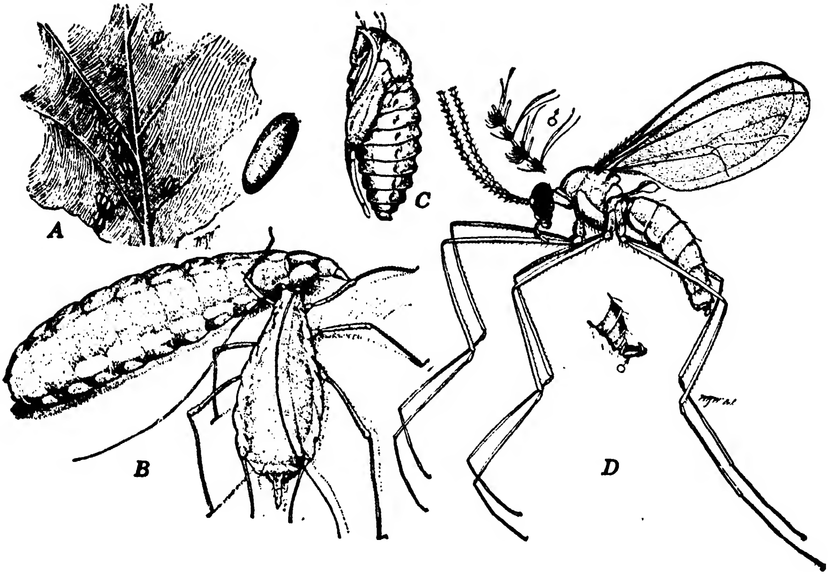


FIG. 370. Predaceous cecidomyiid midge *Aphidoletes meridionalis*. *A*, eggs; *B*, legless maggot approaching aphid prey; *C*, pupa; *D*, adult female, with insets showing male parts. (After Davis)

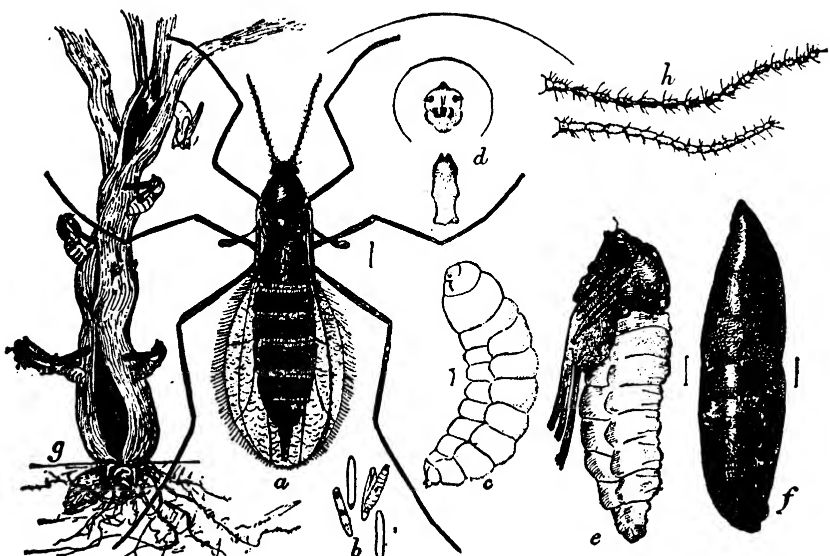


FIG. 371. The hessian fly *Phytophaga destructor*. *a*, female fly; *b*, eggs, one at hatching; *c*, larva; *d*, head and breastbone of same; *e*, pupa; *f*, puparium; *g*, infested wheat stem showing emergence of pupae and adults; *h*, antennae, male and female. (From U.S.D.A., B.E.P.Q.)

many herbs, that the family is known to most observers. The family exhibits a wide range of other habits. Some larvae are predaceous, feeding on mites and small insects, fig. 370; others feed on developing plant seeds; some feed on decomposing organic matter; and still others feed in or on the tissues of leaves or stems of plants. To the latter category belongs the most notable economic species of the family, the hessian fly *Phytophaga destructor,* fig. 371; the larvae feed in the lower stems of grasses and are especially injurious to wheat and barley.

Suborder BRACHYCERA

The adults of this suborder average larger and stouter bodied than the Nematocera and are stronger on the wing. The larvae have hooked or blade-shaped mandibles which work up and down, rather than sideways; the head is frequently much retracted within the thorax, fig. 373, and may have stout internal supports extending far into the body. About fifteen families are represented in North America; some of them are abundant, and in one, the Tabanidae or horseflies, the adults are voracious bloodsuckers.

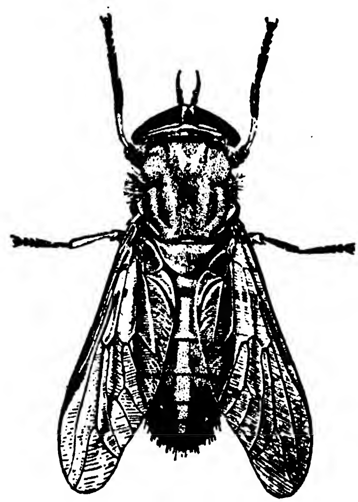


FIG. 372. A horsefly *Tabanus lineolus.* (From U.S.D.A., B.E.P.Q.)

Tabanidae, Horseflies, and Deerflies, Fig. 372. The adults are large-headed stout-bodied insects, often attaining a length of 25 to 30 mm., having strong wings with fairly complete venation and frequently a striking color pattern. The venation features a wide V-shaped cell R_4, which embraces the apex of the wing. The females are bloodsuckers; their mouthparts are developed for cutting skin and sucking the blood which oozes from the wound. The males feed on nectar. Eggs are laid in masses on stems or other objects growing over water; the newly hatched young crawl or drop into their breeding place. The larvae live in swamps or sluggish streams, staying in the bottom mire, and are rarely seen swimming in the clear water. They are predaceous, feeding on snails, insects, and other aquatic organisms. The larval body is tough and leathery, usually white or banded; the head is completely retractile within the thorax. The pupae are cylindrical and brown, normally formed in a mass of peat or dead vegetation which is damp but above the free-water level.

Farm livestock, especially cattle and horses, are often bothered by adult horseflies. Locally these pests may assume major impor-

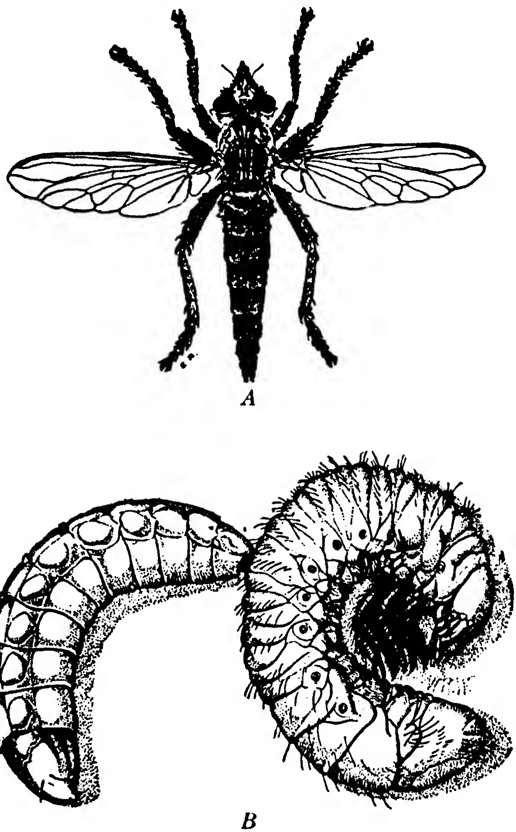


Fig. 373. A robberfly *Promachus vertebratus*. *A*, adult; *B*, legless larva attacking white grub. (From Illinois Natural History Survey)

tance in reducing condition of stock. Many species of horseflies and deerflies abound in marshy areas of the northern and humid montane areas of the continent and discourage vacationers and settlers.

Asilidae, Robberflies. These are also large flies, fig. 373, usually with a humped thorax and elongate abdomen, but in some genera the body is stout, hairy, and brightly colored, resembling a bumblebee.

These flies are predators on other insects, capturing and eating bumblebees and dragonflies in addition to smaller forms. The adults are not easily frightened and are both conspicuous and easily taken in a sweep net. The larvae are found chiefly in soil and rotten wood and are predaceous on insects found there. Some of them are important natural enemies of white grubs and other soil-inhabiting species attacking cultivated crops, fig. 373.

Mydaidae, Mydas Flies. This is a small family, but it contains some of our largest and showiest species. The antennae are clubbed, and the wings have a modified venation, the ends of many veins bending forward towards the anterior margin of the wing. The common eastern species *Mydas clavatus,* is black with an orange band and has a wing spread of 155 mm. The larvae, resembling large asilid larvae, are predaceous and found in rotten logs.

Other families of the Brachycera contain species of great diversity as regards structural peculiarities and habits. Most of them are predaceous on other insects in both adult and larval stages and have free pupae; larvae of most species live in rotten logs or in soil and pupate there.

Suborder CYCLORRHAPHA

This is by far the largest of the three suborders of Diptera. It contains over forty families, many of them composed of a large number of species. For the most part the adults are relatively short and stout bodied, having broad wings in which vein R_{4+5} is undivided, M_2 has atrophied, and Cu_{1b} is only a short recurved stub. The antennae are usually three-segmented, the third segment bearing a style or arista. The larvae have practically no external sclerites of the head capsule remaining, so that the head appears to be only a conical membranous anterior segment of the body. The two mouth hooks (mandibles) are connected with a complex internal pharyngeal skeleton, fig. 377, which provides the attachment basis for muscles controlling feeding. The pupae are formed within the last larval skin, which hardens to become a puparium; the adult pushes off the anterior end of this at eclosion.

Syrphidae, Flower Flies, Syrphid Flies, Fig. 374. Small to large flies characterized by the upturned ends of some of the wing veins, and the presence of a veinlike thickening or *spurious vein* in front of media. These flies feed almost exclusively on flowers and have a remarkable

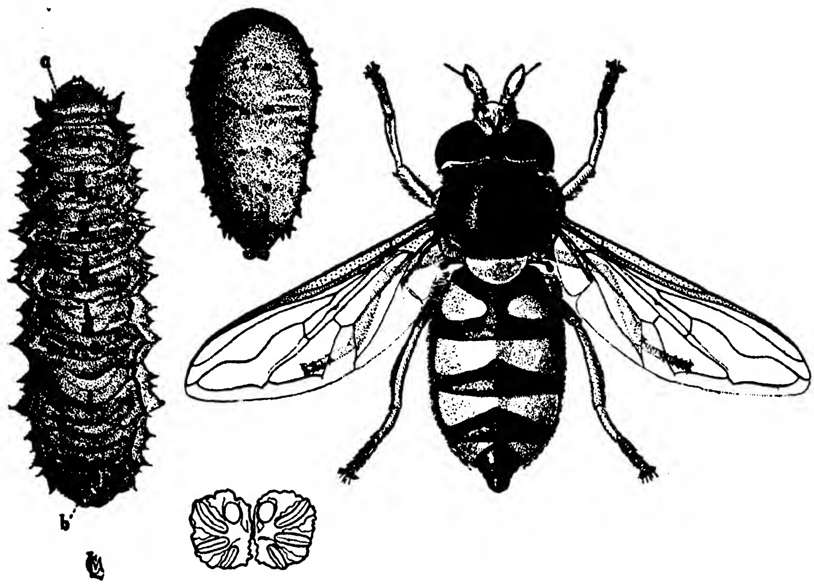


FIG. 374. A flower fly *Didea fasciata*. Right, adult; left, larva; center, puparium; *a*, anterior spiracle; *b*, caudal spiracles. (After Metcalf)

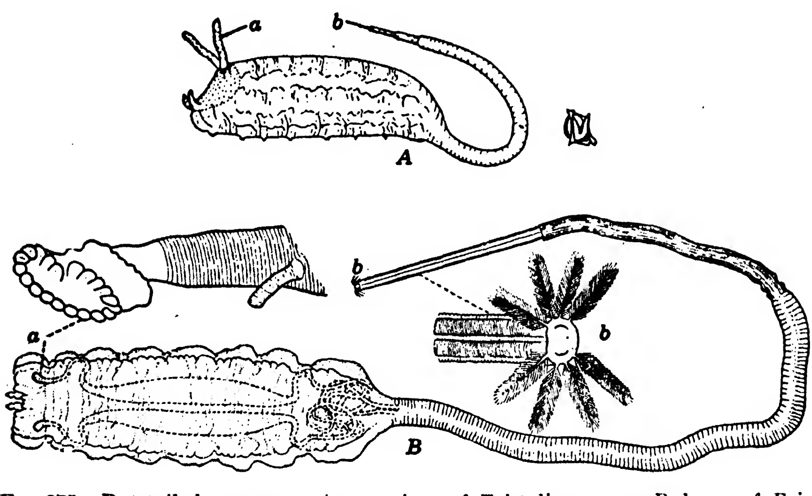


FIG. 375. Rat-tailed maggots. *A*, puparium of *Eristalis aeneus*; *B*, larva of *Eristalis tenax*. *a*, anterior spiracle; *b*, posterior spiracles on long "rat-tail." (After Metcalf)

ability for hovering apparently motionless in the air. Many are brilliantly striped or marked with yellow, red, white, and black; among the family are found mimics of various wasps, bumblebees, and other bees. The larvae are extremely diverse. Many feed on aphids, crawling from colony to colony and devouring huge numbers of individuals. Other species feed in decaying liquid organic matter, for example the rat-tailed maggots of the genus *Eristalis,* fig. 375.

In these maggots the posterior spiracles are situated at the end of extensile "tails" that can be extended to the surface of the food and so provide a contact with air. Other larval foods include debris in burrows of wood-boring insects, leaves and sheaths of grasses, and debris in nests of bumblebees and wasps. Larvae of two species are serious pests of bulbs, eating out the centers of planted tulips and related species.

The Syrphidae is one of a small group of families placed in the Cyclorrhapha, in which the emerging adult does not push off the cap of the puparium; at the time of eclosion the puparium simply splits down the dorsum as do those of the Brachycera which have puparia. Families in this group, however, are most closely related to the Cyclorrhapha on the basis of adult venation, and particularly the well-developed internal pharyngeal skeleton of the larvae.

Typical Cyclorrhapha

In addition to the small group of families related to and including the Syrphidae, the Cyclorrhapha contains a large number of families which are extremely difficult to identify. It is impractical in this discussion to take the student into a detailed account of many of these, and so only a few examples are given, stressing mainly the biological features.

Tephritidae; Fruit Flies. Here belong many brightly colored species frequently with mottled or banded wings. The larvae of several species feed in the seed heads or fruits of many plants. Important commercially are the cherry-fruit fly *Rhagoletis cingulata,* whose maggots tunnel in cherry fruits, and the apple maggot *Rhagoletis pomonella,* fig. 376, which tunnels through apples. The Mediterranean fruit fly *Ceratitis capitata* is a tropicopolitan species that feeds in citrus fruits; it was discovered in Florida in 1929 but was apparently exterminated in a vigorous eradication campaign costing about six million dollars.

Fig. 376. The cherry fruit fly *Rhagoletis cingulata*. *a*, fly; *b*, maggot; *c*, anterior spiracles of same; *d*, puparium; *e*, posterior spiracular plates of pupa. (From U.S.D.A., B.E.P.Q.)

Drosophilidae, Vinegar Gnats, Fig. 377. These are small flies which are common at times in most houses and stores. The larvae breed in decaying fruits and other organic materials. *Drosophila melano-*

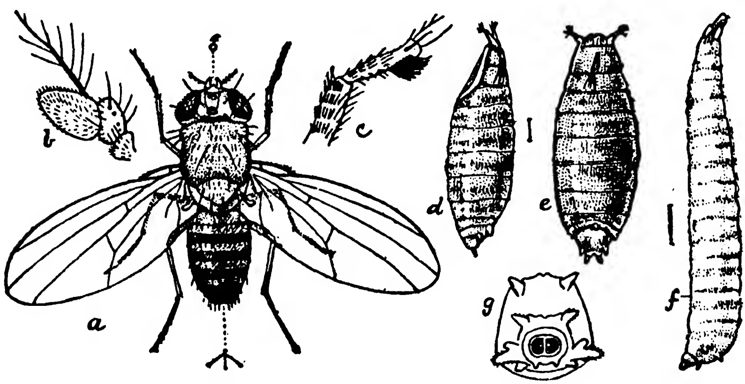
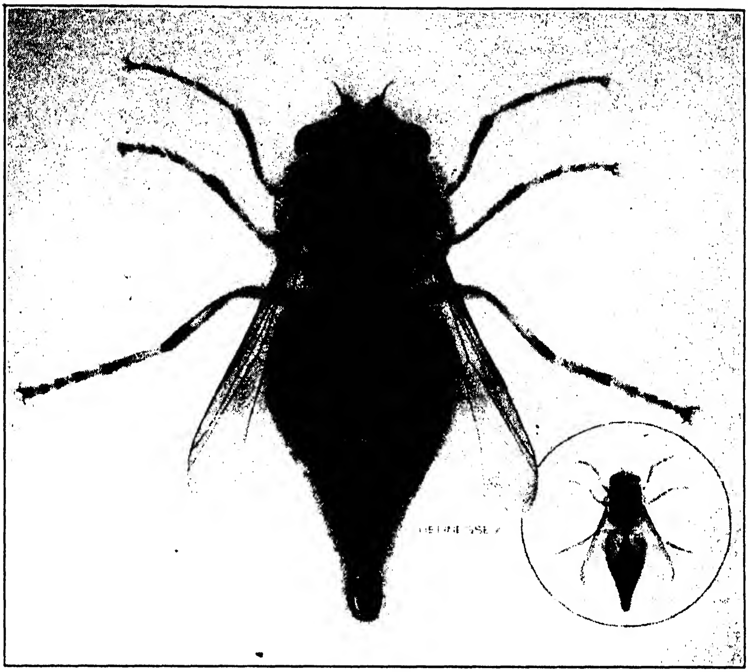


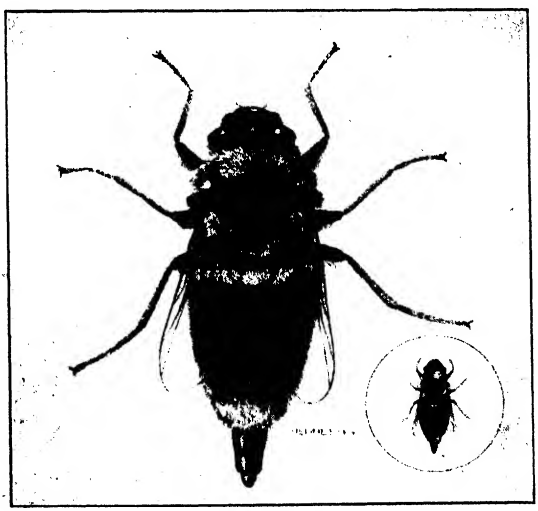
Fig. 377. Vinegar gnats *Drosophila ampelophila*. *a*, adult; *b*, antenna of same; *c*, base of tibia and first tarsal joint of same; *d*, puparium, side view; *e*, puparium from above; *f*, full-grown larva; *g*, anal spiracles of same. (From U.S.D.A., B.E.P.Q.)

gaster has been used as an experimental subject by geneticists and from the standpoint of chromosome and gene mapping is undoubtedly the best-known animal in the world.

Gasterophilidae, Bot Flies. These are moderate-sized flies about the size of a honeybee, somewhat hairy in appearance, and are banded



A



B

Fig. 378. Bot flies. *A, Gasterophilus intestinalis; B, G. haemorrhoidalis.* (From Canadian Department of Agriculture)

with black, yellow, or red, fig. 378. The larvae are internal parasites of horses, mules, man, and some of the larger wild mammals. In North America we have only the single genus *Gasterophilus*, represented by three species which infest horses. The horse bot fly *G. intestinalis* lays its eggs on the hairs of the horse's legs and forequarters. When the horse licks these eggs, they hatch, and the young larvae work their way through the mouth and throat tissues into the horse's stomach. Here the young bots attach to the lining and feed, growing into stout spiny grubs 15 mm. or more in length. They pass the summer and winter in the horse; in spring they loosen their hold, are passed by the horse, and pupate in the ground. The adults emerge in a few weeks.

Muscidae, the Housefly and Its Allies. This family contains probably the world's commonest and most ubiquitous insect, the housefly *Musca*

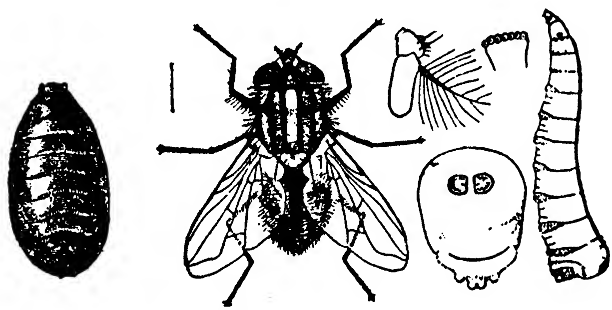


FIG. 379. Stages of the housefly *Musca domestica*. Puparium at left; adult next; larva and enlarged parts at right. (From U.S.D.A., B.E.P.Q.)

domestica, fig. 379. Housefly larvae are white maggots which breed in many types of decaying organic matter. The adult flies transmit several dangerous and widespread diseases, including typhoid fever, several kinds of dysentery, cholera, and trachoma. Another widespread member of this family is the stable fly *Stomoxys calcitrans*, the adult of which inflicts a painful bite and attacks man and domestic animals. Its larvae breed in decaying organic matter; rotting piles of new grass and lawn clippings and manure are high on the list of favorites.

Anthomyiidae. Members of this family are similar in general appearance to the housefly. Economic species in the family include the onion maggot *Hylemya antiqua*, fig. 380, and the cabbage maggot *Hylemya brassicae*, which feed on the roots of their respective hosts.

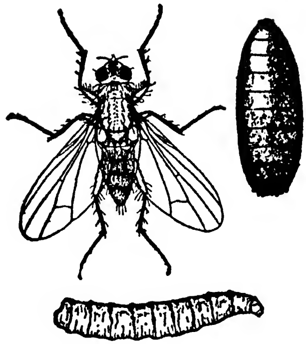


FIG. 380. Life history stages of the onion maggot *Hylemya antiqua,* adult, larva, and puparium. (From Illinois Natural History Survey)

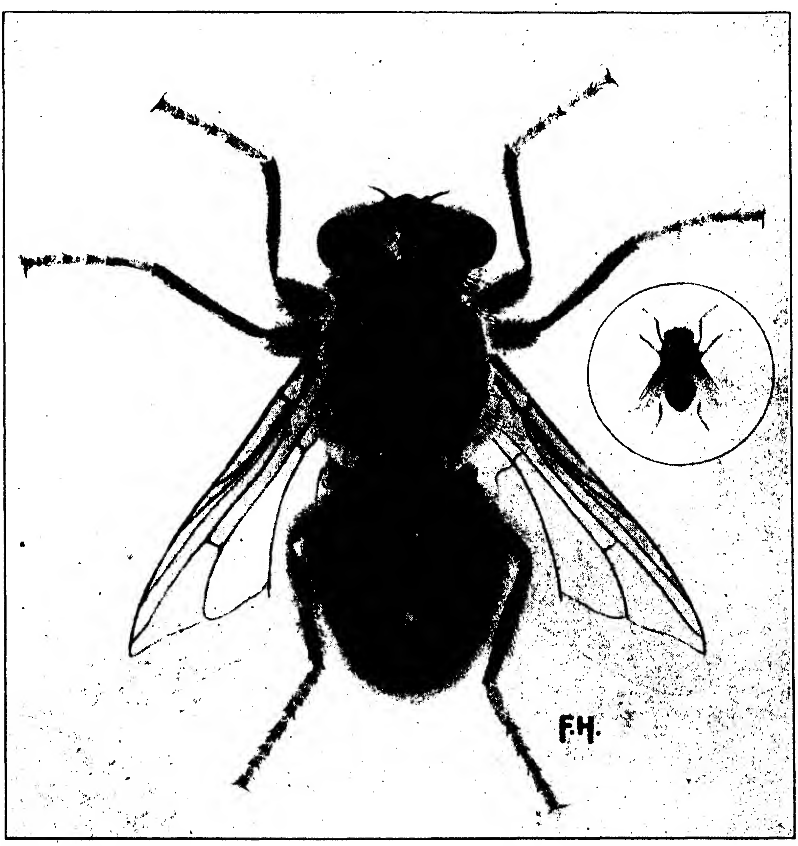


FIG. 381. A warble fly, the adult of the common cattle grub *Hypoderma lineatum.* (From Canadian Department of Agriculture)

Oestridae, or Warble Flies, Fig. 381. These are a small group of fast-flying fuzzy bumblebee-like flies, parasites of mammals; some of them have a life cycle as specialized as that of the Gasterophilidae. Many species have a simple life cycle. For example, the sheep bot fly *Oestrus ovis* deposits young larvae in the nostrils of sheep; the larvae migrate into the sinuses and horns, where they mature. The mature larvae escape to the ground through the sheep's nostrils and pupate. Much more complex is the life cycle of the northern cattle grub

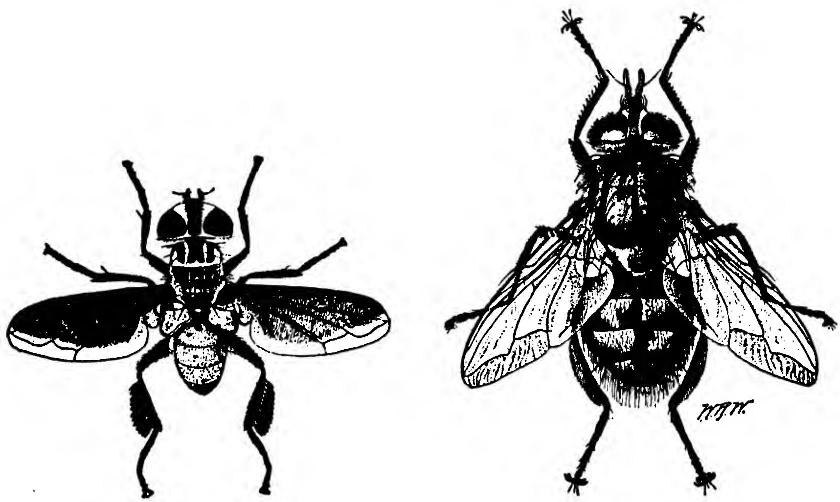


FIG. 382. Tachina flies. At right, *Winthemia quadripustulata,* a parasite of Lepidoptera larvae; at left, *Trichopoda pennipes,* a parasite of Hemiptera. (From U.S.D.A., B.E.P.Q.)

Hypoderma bovis, which attacks cattle. The fly lays eggs on the hairs of the hind legs or flank of the animal. The larvae soon hatch, crawl down the hair, and burrow beneath the skin, making their way slowly through connective tissue to the oesophagus; this journey takes about 4 months. After 3 months' development in the oesophagus the maggots (still fairly small) journey through connective tissue again and come to rest beneath the skin in the lumbar region. Here the larvae attain most of their growth, each causing a swelling called a warble, provided with a small hole through the skin. Through this the larva first obtains air while maturing and then escapes to the ground for pupation.

Tachinidae, Tachina Flies, Fig. 382. This is one of the largest families of Diptera. All its members are parasitic on insects and attack larva or adults of many orders, especially lepidopterous larvae. Many members of this family have been propagated and introduced into various parts of the world in an effort to hold in check some injurious insect. The adult females of many species lay their eggs directly on the host; when they hatch, the maggots bore into the host body and feed on its tissues. In other species the eggs are laid on foliage; if this foliage is eaten by a larva of the host species, the parasite eggs hatch in the alimentary canal of the host, and from there the young larvae bore into the body cavity where development takes place. When mature, the parasite larvae either pupate in the host body or leave it and pupate in the ground.

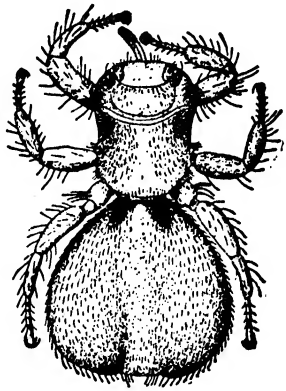


Fig. 383. The sheeptick *Melophagus ovinus.* (From Kentucky Agricultural Experiment Station)

Series Pupipara. Here belong three families, each containing only a few species, which live as ectoparasites on the bodies of birds or mammals. So far as known, all members of the Pupipara have the feature, very unusual among insects, of uterine development of the young. The larvae are retained in the body of the female in a special uterine pouch and nourished on glandular secretions. When mature, the larvae are "born" and glued to the hair of the host, in which position they pupate immediately. The best-known species in North America is the sheeptick *Melophagus ovinus,* fig. 383. This is a wingless ticklike insect common locally on sheep. It belongs to the family Hippoboscidae.

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Order SIPHONAPTERA

Fleas

All adults are wingless, fig. 384, and have long stout spiny legs and short clubbed antennae which in repose fit into a depression along the side of the head. The mouthparts are fitted for piercing skin and sucking blood and consist of a beak, a pair of palps, and a pair of short bladelike maxillae. These insects are small, most of them 2 to 4 mm., but a few species attain a length of 6 to 8 mm. The larvae are slender and wormlike, fig. 385. They have round heads, no legs, and long hairs on each body segment. The segments of thorax and

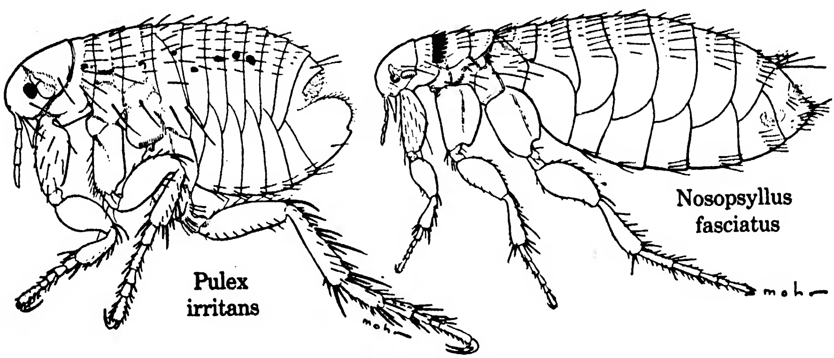

FIG. 384. Two common fleas. (From Illinois Natural History Survey)

abdomen are similar in appearance. The mouthparts are minute and inconspicuous, of the chewing type. The pupae are formed in a cakelike cocoon made of earth or grass.

Fleas feed on the blood of mammals or birds and are found on the body of the host or in the nest or runways of the host. The eggs

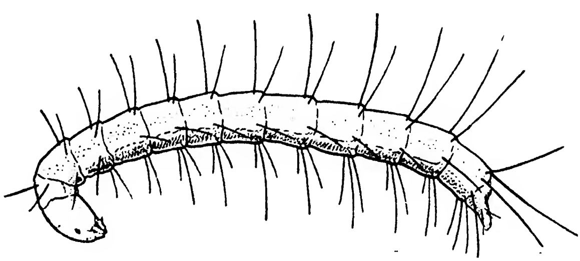

FIG. 385. Larva of a flea. (From Illinois Natural History Survey)

are minute, whitish, and oval. They are dropped by the female either on the host or in the nest. The eggs have no adhesive, so that, if laid on the host animal, they slip through the hair and fall into the litter of the nest or retreat, where they soon hatch. The larvae live in the soil or debris in the nest and feed on debris or grass. When full grown, the larvae spin an irregular cocoon in the nest of the host and pupate. The eggs, larvae, and pupae are seldom seen except by diligent search.

The adult fleas of most species are extremely active. They slip through hair or feathers with great ease; and in many species the body has combs of spines which further aid this progress. In some species the adults stay on the body of the host almost all the time; in others the adults stay in the nest and get on the host only for feeding periods. For this reason it is necessary to collect both from

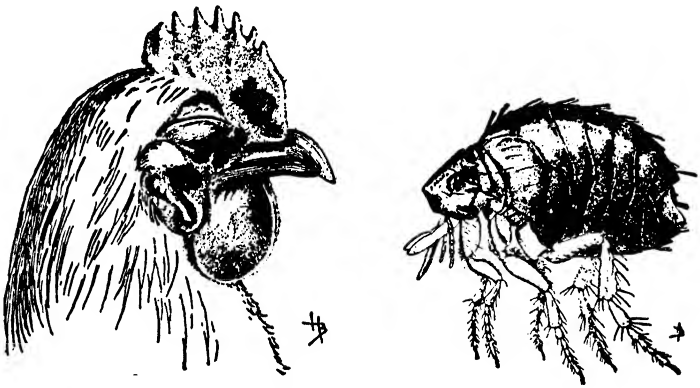

FIG. 386. The sticktight flea *Echidnophaga gallinacea*. Left, infested head of rooster (dark patches are clusters of fleas); right, adult female. (From U.S.D.A., B.E.P.Q.)

the bodies and in the nests of the hosts to be sure of finding all the species connected with it.

The order Siphonaptera is not a large one. The North American fauna includes about sixty genera and over two hundred species. The great percentage of these occur with native mammals, especially various kinds of mice, shrews, ground and tree squirrels, gophers, and rabbits. Bears, beavers, coyotes, and many others support a flea fauna. A few fleas prey on birds and occasionally are a pest of domestic fowl.

A few species of fleas are of especial importance to man. The dog and cat fleas, *Ctenocephalides canis* and *C. felis* and the human flea *Pulex irritans* attack man and invade dwellings, causing great discomfort and inconvenience. The bites inflicted by the fleas are painful, usually cause hard itching swellings, and may be the source of secondary infections through scratching. Most important of the fleas are certain rat species, particularly *Xenopsylla cheopis* and *Nosopsyllus fasciatus*, which transmit the dread bubonic plague from rats to man. In their role as disseminators of this disease, which many times has spread like wildfire through crowded cities in many parts of the world, fleas have been responsible for millions of human deaths. At present, public-health organizations all over the globe keep close watch on the rat–flea–plague focal points, in an effort to break up new incipient outbreaks of the disease, through control of the rats and fleas.

Two economic species, the sticktight and chigoe fleas, have unusual habits in contrast with other fleas. The adults of both species are minute and attach themselves firmly to the host, feeding more or less continuously. The sticktight flea *Echidnophaga gallinacea*, fig. 386, attacks domestic fowl, attaching to the face and wattles. The chigoe *Tunga penetrans* attacks man, especially on the feet. It burrows beneath the skin and forms a painful swelling out of which protrudes only the end of the flea's abdomen. Both species drop eggs to the ground and have typical flea metamorphosis.

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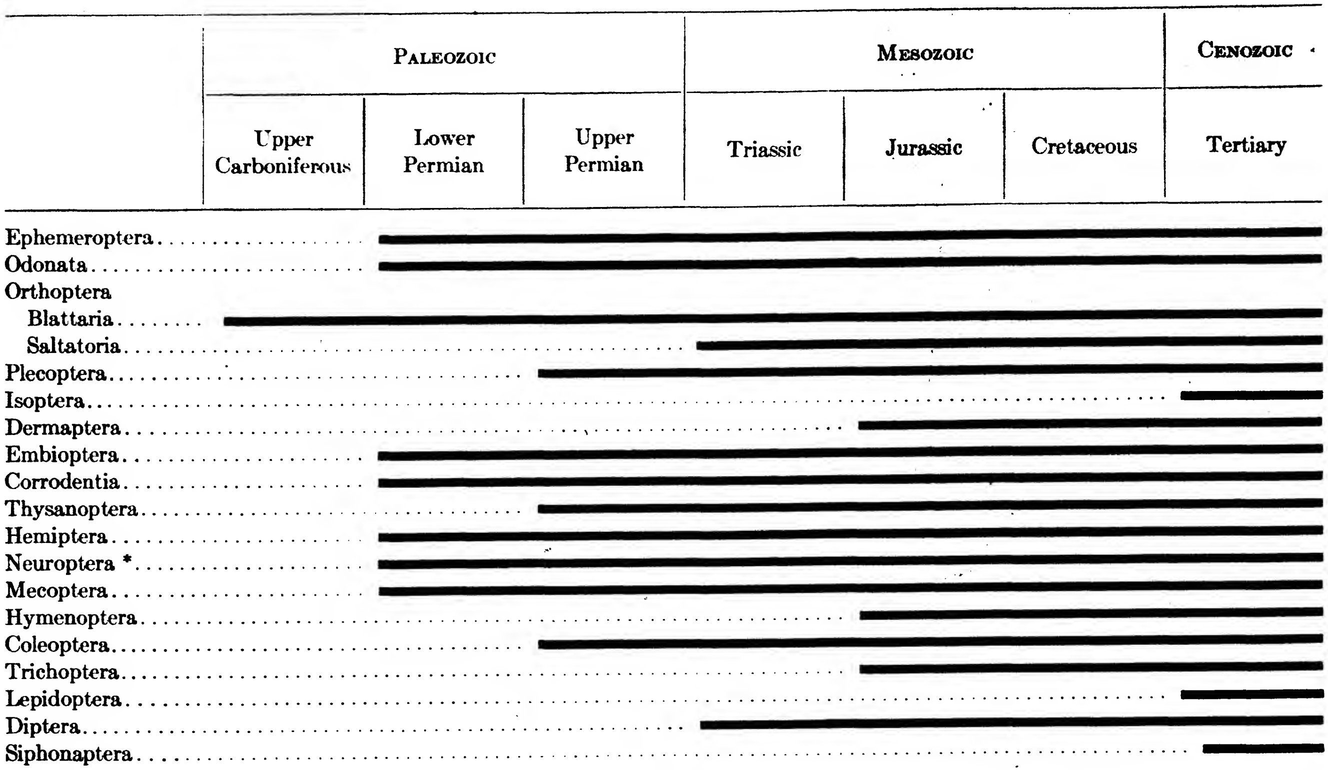
8

Geological History of Insects

The existing insect fauna that we see about us is the result of eons of change and evolution and a struggle for existence among the insects. The struggle has at times been directly between insect and insect, but often it has been a struggle to become adapted to withstand changes of climate. When insects first arose as a group, they were undoubtedly few in numbers of both individuals and species; furthermore, they had only a limited range of ecological conditions under which to live. As the entire organic world developed, there evolved in the insect group members having biological and physiological characteristics enabling them to take advantage of new ecological niches and fill them. If we look over the existing insect fauna as a whole, it is apparent that certain orders, such as the Lepidoptera and Hymenoptera, are large and flourishing, exhibiting a great diversity of structure and habits, but they are relatively young orders in geologic time. We have other orders, for instance, the Mecoptera and Rhaphidiodea, that are represented now by only a few remnants; yet their geological records indicate a beginning of great geologic antiquity. These remnants, like the horsetails and ginkgoes of the plant world, are lonely survivors of what may have been once great orders. Some ancient orders, such as the Palaeodictyoptera, were dominant insect groups in the geologic past, but apparently were unable to change with climate or compete with new forms and are long since extinct.

The avenue of discovery for knowledge of this past history is through fossil remains from strata, or layers of rock, representing the various periods of geologic time. Insect fossils are not found in so many places as are fossils of some other groups because of special conditions needed to insure adequate preservation. Because of their small size,



* In the broad sense, including also Megaloptera and Raphidiodea.

FIG. 387. Geological ranges of the larger present-day insect orders. (Data kindly furnished by Dr. F. M. Carpenter)

the delicacy of their parts, and the minute nature of identification criteria, insect remains must be preserved in a medium of extremely fine texture to provide a grainless matrix. Satisfactory materials are

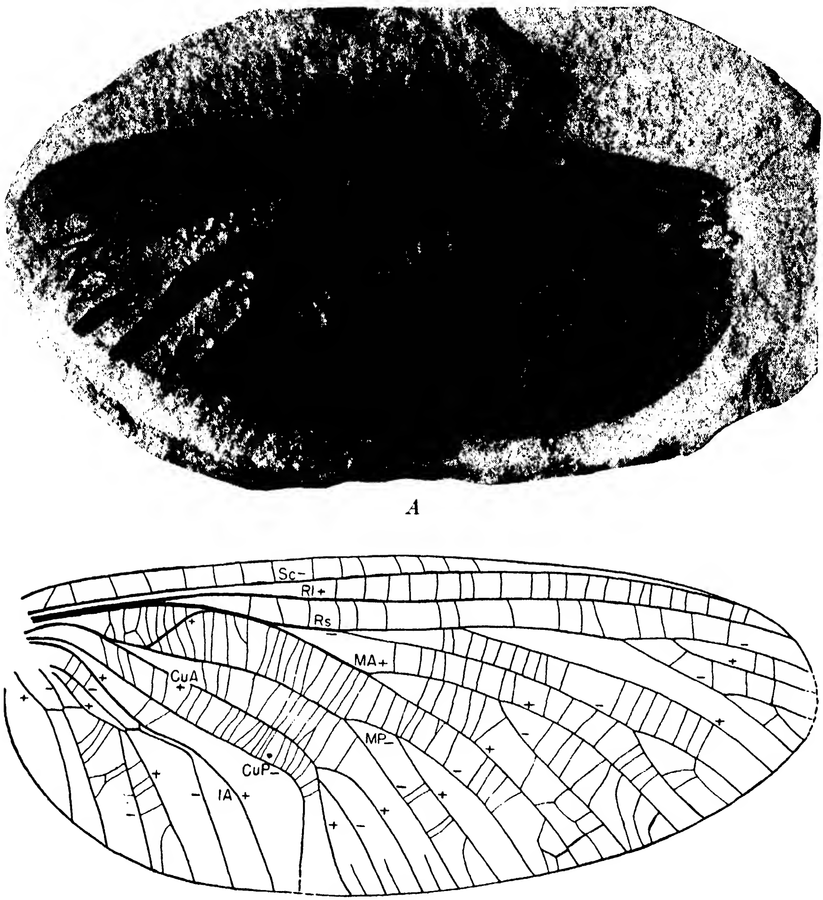


FIG. 388. A fossil from an iron nodule, Mazon Creek, Ill.; hind wing of the paleodictyopteran *Lithoneura mirifica,* a probable relative of an ancestral mayfly. *A,* photograph of fossil impression; *B,* reconstruction of venation. (After Carpenter)

mud and volcanic ash, resulting in shales; concretions; fine humus, such as coal; and resin of coniferous trees, giving amber. Fossil-bearing deposits have been found in scattered localities all over the world. Some in North America are productive of valuable additions to the record. Along Mazon Creek, near Morris, Ill., are found iron nodules, or concretions, containing Pennsylvanian (Paleozoic) insects. Near Elmo, Kan., a deposit has been explored containing large numbers of Permian insects. In several localities in Colorado and Washington occur deposits containing abundant fossils of Eocene and

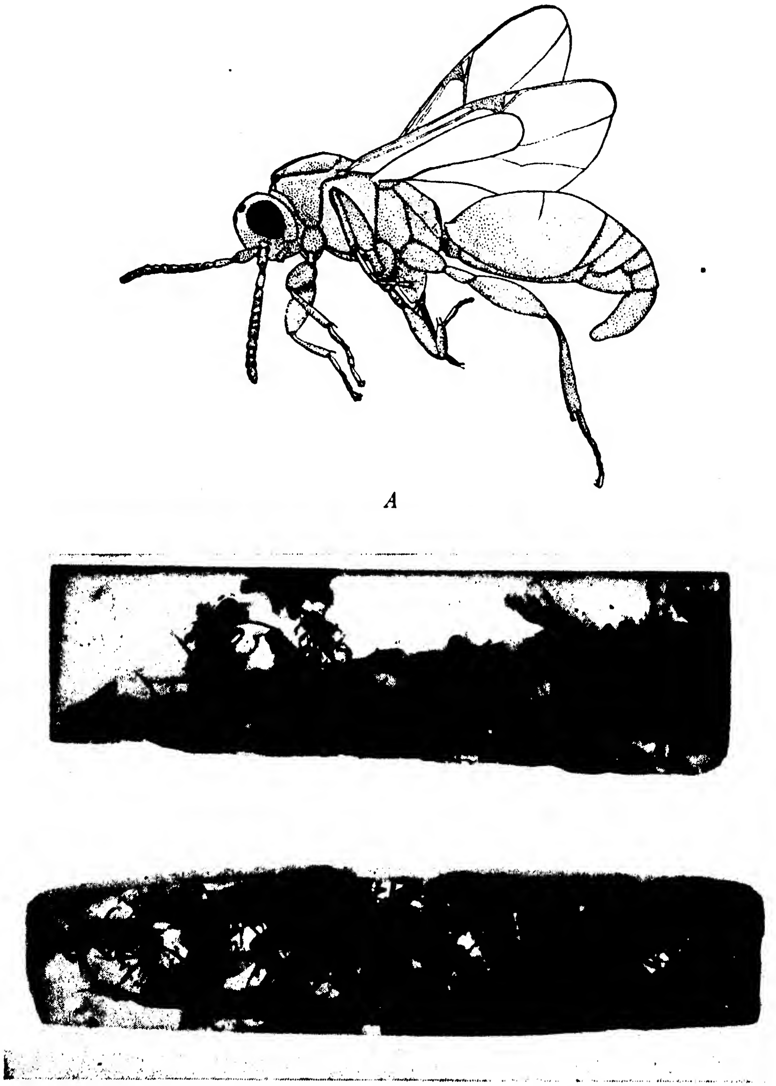


FIG. 389. *Cryptoserphus succinalis,* a hymenopteron described from Baltic amber. *A,* drawing made from specimen in the amber block shown in *B.* (After Brues)

Miocene insects (Cenozoic), and other deposits containing a few Mesozoic forms. In northern Manitoba there have been located deposits of amber containing many insect remains thought to be Cretaceous in origin.

TABLE 5. CONDENSED GEOLOGIC TIMETABLE REPRESENTED BY THE FOSSIL RECORD

Eras		Remarks
Cenozoic—Modern life		
Glacial—Pleistocene		Age of man, extending to present
Tertiary	Pliocene, Miocene, Oligocene, Eocene	Age of mammals and flowering plants. Bloom of modern insect genera
Laramide mountain-making interval		
Mesozoic—Medieval life		
Cretaceous, Jurassic, Triassic		Age of reptiles. Rise of specialized orders and modern insect families, including some modern genera. Rise of primitive mammals and of flowering plants
Appalachian mountain-making interval		
Paleozoic—Ancient life		
Permian		Rise of modern orders of insects
Pennsylvanian, Mississippian	Carboniferous	Rise of primitive reptiles and insects
Devonian		Age of sharks. First extensive land floras, first amphibians
Silurian, Ordovician, Cambrian		Age of invertebrates. Rise of land plants
Killarney mountain-making interval		
Proterozoic—Age of primitive invertebrates		Few primitive invertebrates
Archeozoic—Age of unicellular life		Primitive plants

In the main, wings are the principal insect structures clearly preserved in fossils. In amber insects other structures are frequently seen with great clarity, resembling a balsam preparation on a microscope slide, fig. 389. In shale and concretion specimens, however, it is only occasionally that the structure of body and appendages can be determined.

Although there are tremendous gaps in the known insect fossil record, enough has been discovered to gain a fair idea of the general trend. In the brief account that follows, the main emphasis has been placed on the biological and ecological implications of the evidence. This is given in relation to the geological timetable in general use, Table 5, with which the student should become familiar.

Table 5 represents the period of evolution of all known life on the earth. This time is established by various geologists and physicists at from 500 to 1500 million years. If we take the thickest known deposits laid down in all these periods and add them together, it would result in deposits 70 miles deep. Such a mass of material means the wearing away to sea level, one after another, of more than 20 ranges of mountains like the present European Alps or American Rockies. Visualize the amount of time it would take erosion to do this, and then add the much longer quiescent periods when the low-lying lands furnished little sediment, and we have some idea of this length of time.

EARLY GEOLOGIC ERAS

Several long chapters passed in the geological record before insects appeared. The first forms of life were unicellular organisms which probably began before the Archeozoic. From these evolved the many kinds of multicellular plants and animals. Through the Archeozoic and Proterozoic, life was exclusively marine. The same was true through the Cambrian and Ordovician periods of the early Paleozoic, when the seas were shallow, extensive, and warm. At this time the Arthropods were well developed, represented by Trilobita, complex Crustacea, and Eurypterida. All the animal phyla as we know them today are represented in the fossils of these periods, including the first vertebrate fossils, primitive fish. It is interesting to speculate on the appearance of the world at this time. The land was barren, at most with encrustations of lower plants, and away from the seas probably had not even these signs of living matter.

In the Silurian came the first feeble beginnings of a land biota, with the appearance in the fossil record of a few land plants and the first air-breathing animals, scorpions, and myriapods. These animals were probably littoral, occurring along the beaches in the warm moist Silurian climate.

The Devonian and Mississippian periods are termed the "Age of Sharks" by geologists. Although these animals attained great evolutionary development, the event of most interest from an entomological viewpoint was the rise of land floras. Forests developed along stream edges and in lowlying swamps. This development, providing shelter, humid conditions, and food, was essential for the extension of animal life beyond the limited areas of the beaches. The fossil record of the land fauna is fragmentary but demonstrates the presence of myriapods and amphibians. It is likely that in this period primitive insects not only had evolved as a class but also may have developed fairly suc-

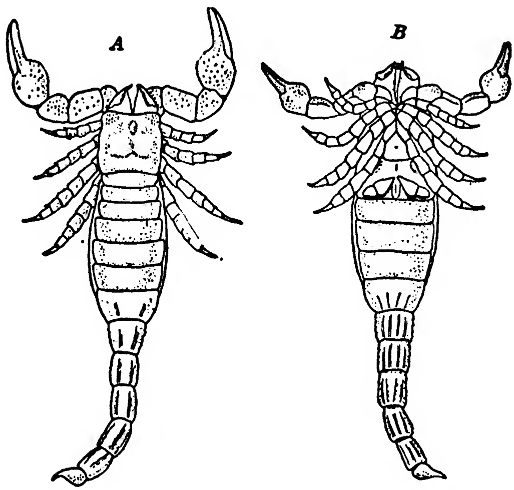


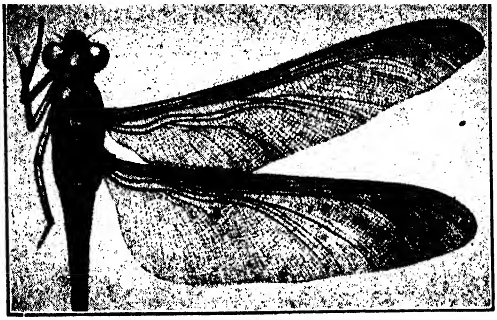
FIG. 390. Restoration of two Silurian scorpions, among the earliest known air-breathing animals. The similarity between these and recent forms is remarkable. *A*, dorsal view of *Palaeophonus nuncius; B*, ventral view of *P. hunteri.* (From Pirsson after Pocock)

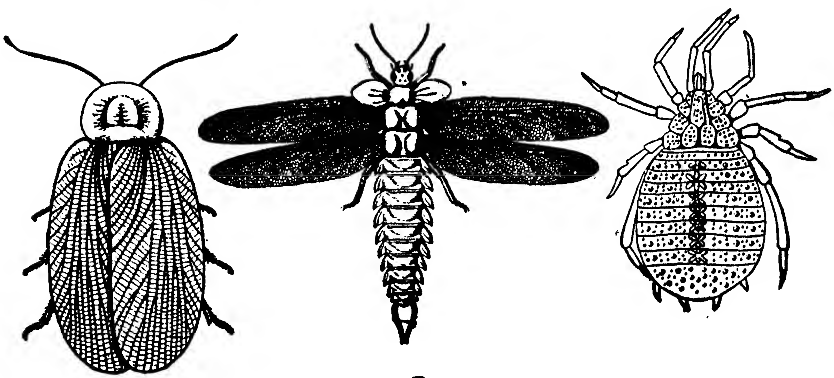
cessful flight. We may infer from the scarcity of terrestrial animal fossils in this period that, even after the forests had become stabilized, their successful invasion by land animals was a slow process.

LATE PALEOZOIC ERA

Pennsylvanian. Insect fossils first appear in the Pennsylvanian. These were well developed, having wings with extensive venation; distinctive head organization including antennae, eyes, and mouth-parts; a typical thorax with three pairs of legs; and an abdomen with a pair of long cerci. Since these oldest-known fossil insects are so highly developed, it is logical to assume that insects had their origin in some earlier period. About fifteen hundred species of insects are known from the Pennsylvanian, fig. 403, representing the

Paléaodictyoptera, Protodonata, Blatteria (cockroaches), and some other orders which are of doubtful status. Cockroach fossils are so abundant in this period that it is called the "Age of Cockroaches."





B

Fig. 391. Pennsylvanian insects and a spider. *A,* the largest known insect of all time, *Meganeuron monyi,* from the coal measures of Belgium. A reconstruction by R. J. Tillyard. About one-seventh natural size. *B,* left, a cockroach *Aphthoroblattina johnsoni;* center, a primitive insect *Stenodictya lobata;* right, a spider *Eophtynus prestwichii.* (After Schuchert and Dunbar, "A Textbook of Geology," Pt. II, Historical Geology)

It is thought that the nymphs of all these insects were aquatic or semiaquatic and lived in the swamp pools which were extensive in many areas of the barely emergent continents. Here also insects attained their greatest size, including Protodonata (primitive dragonflies) with a wing span of 29 inches.

At no other time in the geologic history of the world have conditions been so ideal for insects. The climate was warm and humid,

Fig. 392. Pennsylvanian flora and amphibia, as restored by J. Smit. In the background are *Sigillaria,* with tree ferns and conifers in the middle distance. In the foreground are *Calamites* and seed-bearing fernlike plants. Amphibia are represented by a small four-limbed microsaurian (*Keraterpeton*), a large-headed form (*Loxomma*), and a snakelike gill-bearing stegocephalian (*Dolichosoma*) from Linton, Ohio. (From Schuchert after Knipe, "A Textbook of Geology," Pt. II, Historical Geology)

with neither winters nor dry seasons. Swamps, lagoons, and estuaries were well forested and relatively widespread, fig. 392. Insects and amphibians dominated the swamps. The competition between these two groups must have been ferocious for, whereas the adult amphibians undoubtedly fed on insects, many of the large predaceous insect nymphs surely fed on the vulnerable larval amphibians. This competition, together with competition among the insects themselves, must have exerted a strong evolutionary pressure toward the development

FIG. 393. Photograph of a fossil of a primitive insect *Dunbaria fasciipennis*, from the Early Permian period (Late Paleozoic). (From Mavor, "General Biology," by permission of The Macmillan Co.)

of large size in insects. The climate would not discourage this tendency but rather encourage it by providing uniform growing conditions throughout the year.

Permian. This period was one of the most critical in the history of the organic world and changed the direction of evolution in almost every group of plants and animals. Extensive mountain making, called the Appalachian Revolution or orogeny, in late Pennsylvanian and continuing through Permian times, wrought great changes in climate, resulting in widespread cold and prevalent arid conditions. This change, following the warm moist climates of the Pennsylvanian, spelled doom to many specialized stocks, especially those that developed toward gigantism. The surviving forms were mostly the smaller generalized stems which had the inherent possibility of becoming adapted to new environments.

Fossil evidence certainly shows that such a reduction and change took place among the insects. Thousands of Permian fossils collected at Elmo, Kan., have given us a very good picture of the fauna. The insects were smaller, and many of the old archaic forms had practically disappeared. Here are found the first representatives of many modern orders, the beetles, scorpionflies, true dragonflies, mayflies, very primitive bugs, psocids, and orthopterons. Later in the Permian, other orders are found, including Neuroptera and Diptera. It is to be remembered that these forms were very primitive. The presence of four orders of the Holometabola indicates that complete metamorphosis had been developed in the period. It is considered that this was in response to seasons of drought rather than to cold winters. Amphibians were the dominant animals during the Permian but toward the end dwindled rapidly because of changing climates. Incidentally, the Great Plains have been a stable feature of North American landscapes since this time.

MESOZOIC ERA

Relatively few early Mesozoic fossil deposits have been discovered; hence we have a very imperfect picture of insect evolution in this era. In addition, there was apparently a long period between deposits of the late Paleozoic and early Mesozoic, with the result that there is a marked advance in insects of the Mesozoic in comparison with those of the Paleozoic.

Triassic. In this period, which is the first of the Mesozoic, conditions for land life were very trying, as in the Permian. Great areas were desert or semidesert, caused in North America by the extensive emergence of the continent. Forests were restricted to lowlying areas in river basins and coastal plains. These medieval floras were strange in their varied types of rushes, ferns, cycads, and conifers. This plant world was populated in the main by dinosaurs, a group of reptiles which became dominant and for which the Mesozoic is called the "Age of Reptiles." These were the most extraordinary animals the world had ever seen, as diversified in form and size as are living mammals. Among them were huge swift carnivorous forms; also sluggish duck-billed types feeding on swamp vegetation; other vegetarians had great snakelike necks for browsing on tall trees. In addition to the dinosaurs there were many small reptiles of varied habit and a few very primitive mammals. There varied types were the ecological equivalents in the Mesozoic of the herbivorous, carnivorous, and insectivorous mammals of today.

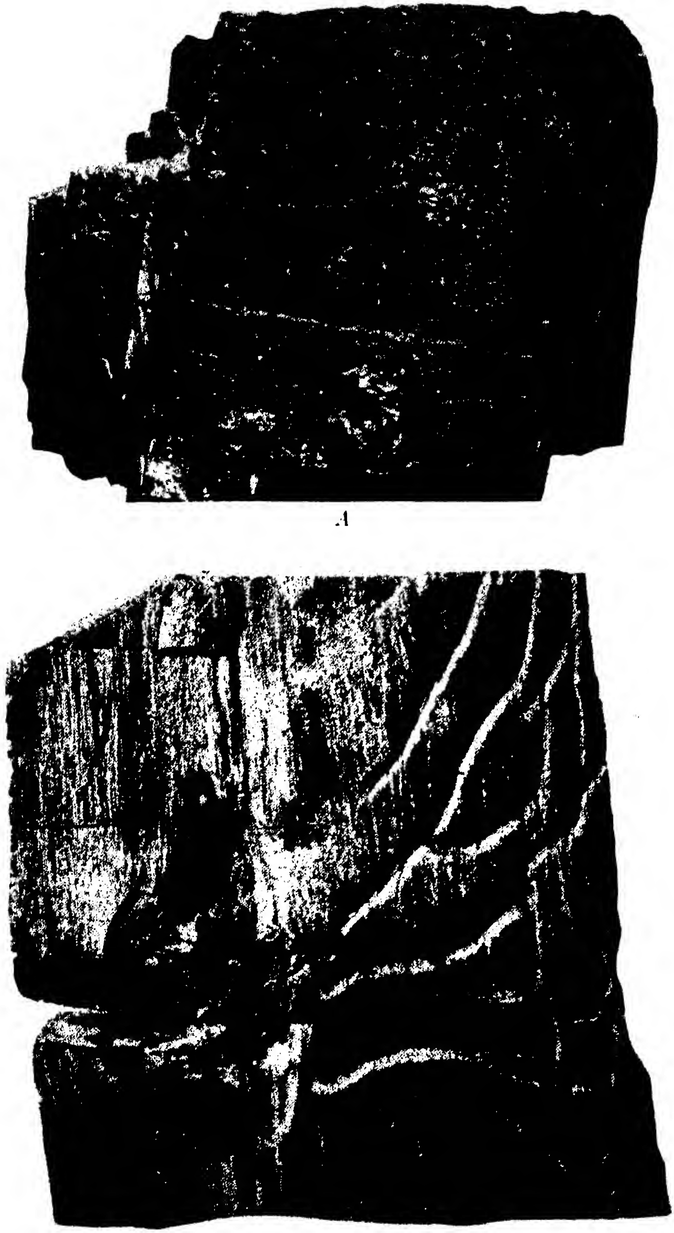
In this period fossils of the true bugs, Heteroptera, are first found, but these forms are so well developed that the order undoubtedly occurred in the Permian. By this time most of the ancient orders such as the Megasecoptera had apparently died out completely, and the general character of the fauna was more like that of today. Many groups had developed specialized habits of feeding familiar to us in present-day insects. A striking example of this is the preservation in petrified Triassic trees of feeding tunnels typical of modern Buprestidae and Scolytidae, fig. 394.

Jurassic. In the early part of this period conditions were somewhat as in the Triassic, but with periods of world-wide lower temperatures. At this time arose the curious assemblage of flying reptiles called Pterodactyls. Some of these were huge, soaring like buzzards. Many frequented ocean shores and probably fed on fish, but small types flitted about over the ground and probably were insect feeders.

The insects were smaller than their present-day relatives. Several orders appear for the first time—Trichoptera, Dermaptera, Hymenoptera, and Thysanoptera, most of their representatives belonging to modern families. In middle Jurassic the climate moderated over the entire world, and insects increased in size and numbers. It is probable that the plant-feeding habit became better established on the varied floras which developed at this time. Plant flowers, however, were inconspicuous, and it is unlikely that many insects visited them.

The Jurassic closed with periods of definite climatic zones and winters, which helped to establish the ascendency of those plant and animal land groups which possessed provision or adaptations for overwintering.

Cretaceous. Much of the modern plant and insect life was established in this period. The Angiosperm flowering plants had begun their ascendency over the spore-bearing floras and the archaic gymnosperms, the cycads and allies, so that by the end of the period 90 per cent of the plant genera were of the woody kinds known today, including elms, oaks, figs, magnolia, beech, birch, and maple. Sedges and grasses appeared. Although most of these were wind-pollinated groups, some of those mentioned and many other genera known from this horizon were undoubtedly insect-pollinated as they are today. The evolution of insect-pollinated plants and pollen- and nectar-feeding insects were complementary developments. This association in



A

B

FIG. 394. Feeding tunnels of *A*, a buprestid beetle, and *B*, a scolytid beetle in petrified Triassic trees, Petrified Forest National Monument, Ariz. (After Walker)

the Cretaceous was only the feeble beginning of a partnership which has proved highly successful for both. Today over 65 per cent of the flowering plants are insect-pollinated, and 20 per cent of the insects, at least in some stage of their development, depend on flowers for food.

The relatively few Cretaceous insect fossils are varied in taxonomic composition and include stoneflies, dragonflies, cockroaches, springtails, midges, aphids, caddisflies, and a large number of parasitic Hymenoptera. Many of these are close relatives, or actually members, of existing genera; some others represent genera of a primitive nature. A few are of exceptional interest because they represent families intermediate between existing families; an example is the collembolan family Protentomobryidae described from the Cretaceous amber of Manitoba, a family having distinctive characteristics yet intermediate in antennal structure and body segmentation between the Recent families Entomobryidae and Poduridae.

The rise in the Cretaceous of many favorable host plants must have encouraged great evolutionary development among phytophagous insects. The appearance of numerous parasitic Hymenoptera indicates that populations of their insect host species were at least fairly large and that the present-day interrelations of the groups had already been established. It is interesting to note that reptiles, which had dominated the land life and much of the aquatic up to this time in the Mesozoic, were rapidly being supplanted by the primitive land mammals.

The Mesozoic ended with great mountain making which again changed the climate all over the world.

CENOZOIC ERA

The Cenozoic prior to the glacial age consists of four distinct periods, the Eocene, Oligocene, Miocene, and Pliocene, collectively sometimes called the Tertiary. The last period of the Cenozoic is the Pleistocene or glacial age. Of great significance in the present distribution of insects were the continental and climatic conditions of the Cenozoic.

Throughout geologic history the shape of the continents as well as their topography has changed. For instance, North America has sometimes been reduced to half its present size and also has been increased far beyond the present margins and has had various connections with Northern Eurasia. North and South America have been connected broadly at some times, widely separated at others. One has only to allow a little freedom of imagination to visualize what this has done to the migration and isolation of floras and faunas.

Through the Tertiary as a whole there occurred a vast development of plant species and diverse kinds of modern birds and mammals. Practically all genera as they are known today were fully resolved. In the case of all these, certain insects had unquestionably become associated with them back in the Mesozoic and continued to evolve along with their hosts. Among the best examples of this are the hemipterous bugs of the family Polyctenidae, which are ectoparasites of bats. The bugs have been associated with bats so long that the parasite bug genera essentially parallel the host bat genera as regards phylogeny and distribution. The host connection of gall-making cynipid wasps, such as the genus *Cynips* with oaks, quite possibly follows the same pattern.

Eocene. In the early part of the Eocene, mountains were very high and climates cool and semiarid. North America seems to have been joined with Greenland and Europe to the east and certainly with Asia to the west, permitting wide radiation of land life throughout the holarctic area. At this time North and South America were connected, and the Greater Antilles were connected with Central America. In late Eocene, North and South America became separated and remained so until middle Pliocene. Later in the Eocene warm and moist climates prevailed, because the mountains had been greatly worn down.

Oligocene. During this period the mountains were worn down, and the lands eroded away to almost sea level. Warm climates were the most widespread of any time in the Cenozoic. Palms and sequoias were abundant. Ants attained large populations; over one hundred species are known, and a fourth of these are identical, or nearly so, with present-day forms. North and South America were completely separated by the Caribbean Sea which entirely flooded the Antilles and Central America.

Miocene. In North America, Europe, and Asia, mountains began to rise again in this period, and the climate grew cooler and drier. Forests were reduced in areal extent, and grasses took possession of the open spaces. This formation of grasslands permitted great development among herbivorous mammals, and probably a similar evolution occurred among grass-feeding insects such as grasshoppers and leafhoppers.

The fullness of modern insect life was attained during this period. Ample evidence of this is contained in the extremely large number of fossils found at Florissant and Creede, Colo., and other localities. These fossils are the remains of insects trapped in volcanic ash which settled in lakes of that time.

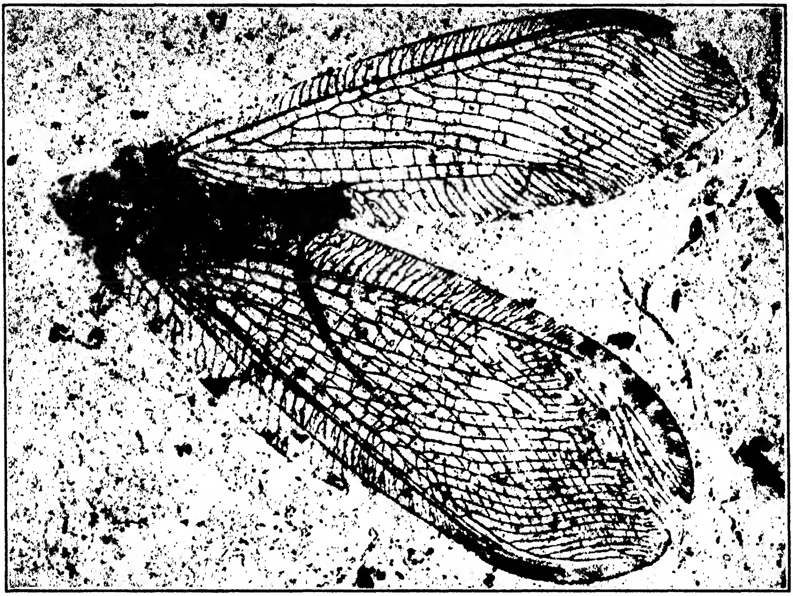


FIG. 395. An osmylid lacewing (Neuroptera) *Lithosmylus columbianus,* from the Miocene shales of Florissant, Colo. (Photograph loaned by F. M. Carpenter)

In middle Miocene a land bridge existed between North America and Asia, but late in the period the bridge with Europe broke between Norway and Greenland. North and South America were separated until late in the period, but the connecting bridge then formed was little used, owing to volcanic activity or tropical jungle barriers.

During the three early periods of the Cenozoic—Eocene, Oligocene, and Miocene—the insect fauna was abundant and varied, and, judging from fossils from many localities, many of the forms were nearly cosmopolitan. In North America there occurred hundreds of genera that are still represented in the present-day fauna, though many of them no longer occur in the nearctic region. Familiar Tertiary genera that still occur in North America include *Tabanus* (horsefly), *Sciara* (fungus gnat), *Tortrix,* (leaf-roller moth), *Hemichroa* (sawfly), *Saperda* (longhorn beetle), and a host of genera in several families of parasitic Hymenoptera, fig. 389.

Pliocene. In western North America mountains were being elevated, and this change brought colder and more arid climates in the Northern Hemisphere. Eastern North America also was elevated and the Mississippi Valley raised to its present height. With these climatic changes only the more hardy or adaptable forms survived in the northern part of the globe. The less hardy either were exterminated or maintained themselves in the warmer climates to the south around the equator. It is likely that some genera actually migrated southward and that others already were living there before the time of climatic changes to the north. Examples of probable migrant groups are many of the large mammals and the tsetse fly *Glossina,* now occurring only in equatorial Africa. In the Miocene these occurred in North America and may have been widespread over the central and northern portion of Eurasia. Another interesting case is the neuropterous family Osmylidae, now restricted to tropical areas, but in the warmer Tertiary climates distributed throughout the holarctic region, fig. 396. As the present-day tropical fauna becomes more completely known, examples come to light of additional genera that are now restricted to relatively small tropical areas, but were widespread in past geologic eras.

Pleistocene, the Great Ice Age. Following the extensive mountain elevation of the Pliocene, there was a temperature reduction over the entire world, the greatest extremes centering around the North Pole. Glaciers were formed in many regions of the world, especially northern North America and northern Europe, and spread southward. The ice in these huge glaciers or ice caps was at least several thousand feet thick. In their extension southward they blotted out all possibility of life over vast areas. This caused a migration of the entire biota southward, compressing the tropical forms into much narrower zones than their range today. Three main glacial periods are recognized, and between each two there was a longer interval with a climate warmer than our present one. This alternation of warm and cold climates caused waves of first one type of flora and fauna and then another to migrate first southward, then northward, over the glaciated areas. For instance, during the coldest periods such Arctic animals as the musk ox ranged as far south as Georgia, and during the warm

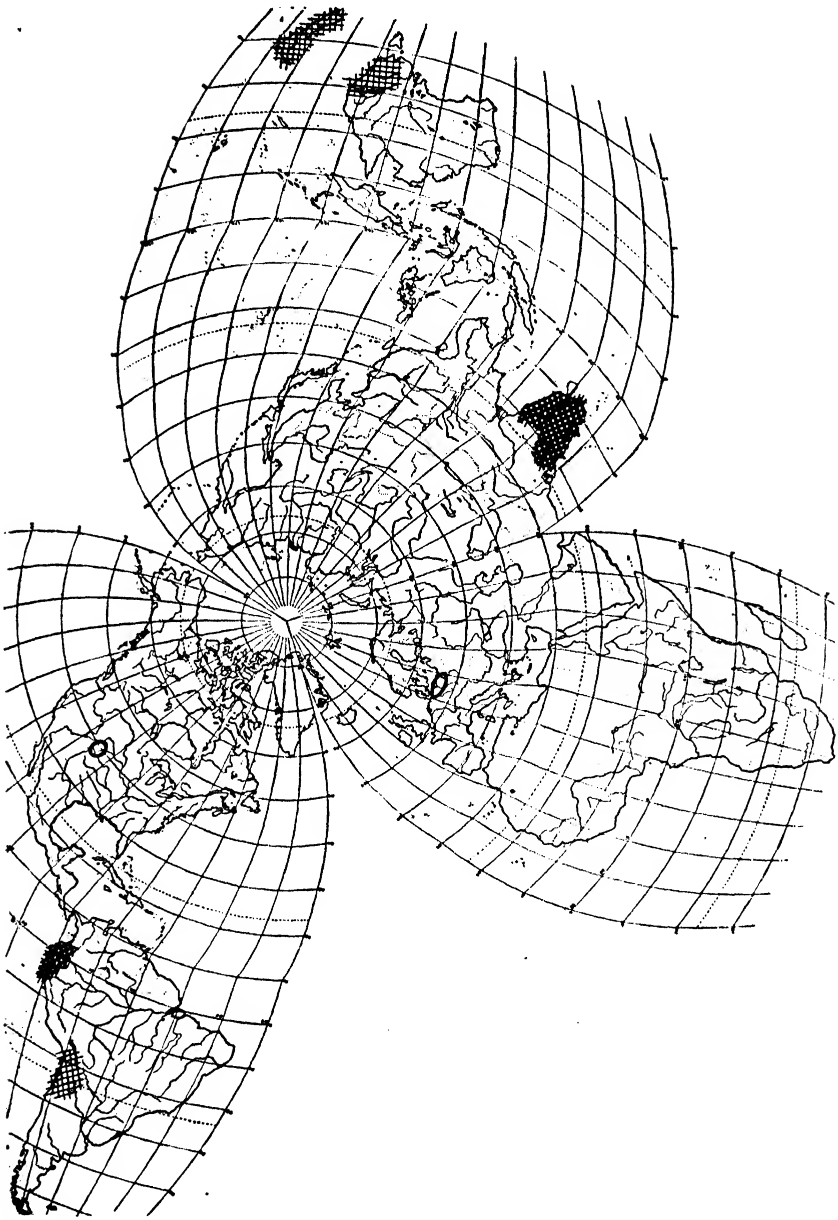


FIG. 396. Known Recent and Miocene distribution of two subfamilies of Osmylidae. Cross-lined area, Recent Kempyninae; checkered area, Recent Protosmylinae; circle in North America, Miocene Kempyninae and Protosmylinae; oval in Europe, Miocene Protosmylinae. (Data compiled from Carpenter, 1943)

interglacial periods the elephant group inhabited the circumpolar area as far north as Alaska.

These glacial movements had an extraordinary effect on the evolution of both the faunas and floras. In the warm periods between two glacial periods a great many species of all groups spread into the temperate holarctic region and became generally distributed over North America and Eurasia. When the climatic pendulum swung toward the colder side and the next glacier formed and began its southward march, this entire heterogenous population moved south again. But at this point it must be remembered that Africa, India, Australia, and the Americas are all south from the North Pole. Hence, some portions of identical populations were crowded from the holarctic area into regions that were immediately isolated. In other words, some individuals of a species migrated into India, some down the Malayan Archipelago, others into Central America. Since there was no land bridge between these regions to the south and the glaciers covered the connecting land bridges to the north, there was no biotic interchange, and the migrant individuals became isolated.

During the long interval of an ice age, these isolated remnants of species gradually changed, and each remnant evolved into a separate species. When the ice receded and temperate climates reigned again in the north, these new forms spread back into the circumpolar land mass of North America and Eurasia. There another east–west dispersal took place. With the onset of the next ice age, the same migration began to different areas to the south. But this time the migrating populations contained many more species than the populations affected by the first ice age. The identical cycle was repeated three times in fairly rapid succession, once for each ice age, each time compounding the species of the northern area. For instance, if we consider a single species of the Pliocene, its division into subsequent species could well be of this order: The first glacial age might well have broken it into four populations each becoming a species; if all migrated north at the end of the first ice age, the second ice age could have broken each of these into four more species, making a total of 16; the third ice age dispersed each of these 16 for a potential total of 64 species. The multiplication factor of four at each migration seems to be a conservative figure, based on the present world distribution of closely related species.

It is believed that at the present we are living in the receding portion of the most recent glacial age, and the ice cap is gradually moving northward as it shrinks. Studies of the insect fauna give considerable weight to this conclusion. Mapping the range and relationship of certain genera indicates that some of the insect genera

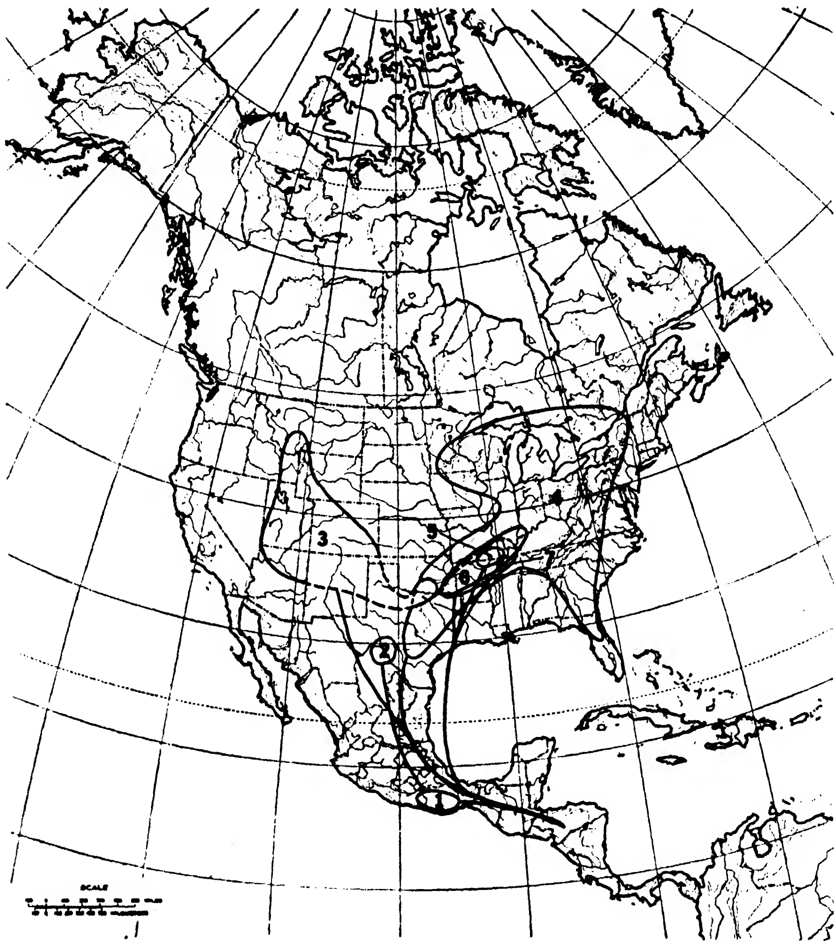


Fig. 397. Migration and evolution of the world species of the *tarsalis* complex of *Ochrotrichia*, a genus of caddisflies. Outlines delineate approximation of range for the species: 1, *tenanga;* 2, *felipe;* 3, *stylata;* 4, *tarsalis;* 5, *contorta;* 6, *shawnee;* 7, *anisca.*

that were pushed south by the last glacial era are following the warmer weather northward. As populations have moved northward again, parts of them have become isolated enough to develop into species or subspecies, whose relationships may point to the direction of migration. Certain of these, for instance, the caddisflies of the genus *Ochrotrichia*, seem to demonstrate clearly a migration route northward from Mexico into temperate parts of the continent, fig. 397.

At the present we are living in a time of rigorous conditions. We have areas of great highlands and mountains; nearly a fifth of the land surface is arid desert; most of the world has marked summers and winters; and the polar regions are covered with remnants of the ice cap. The present insect fauna is the result of evolutionary forces correlated in great part with climatic conditions of the geologic past. We must realize that present climatic conditions are exerting as much pressure on evolutionary trends as at countless other times and will be a factor in molding the insects of future ages.

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9

Ecological Considerations

When we look at life in natural surroundings, we see that the landscape is broken up into different types of interlocking areas, such as prairies, forests, deserts, lakes, and streams. The type of vegetation, that is, whether it is desert, prairie, or forest, is determined by climatic factors of temperature, rainfall, and evaporation. In the main, forests grow in regions having a high rainfall, prairies in regions having lower rainfall, and deserts where rain is scant and evaporation high. Types of aquatic habitat depend on slope, rainfall, and a large variety of local factors including acidity and leaching qualities of the soil, drainage, seepage, and temperature. The vegetation type of the landscape is therefore a reflection of the climate, and widely separated areas having similar climate have the same kind of landscape aspects. Each of these is divided into smaller units. A forest, for instance, has an edge area and may have small open areas or glades scattered through it; in one place the forest may be well drained and high, with a preponderance of oaks and hickories, in another place it may be low and swampy, having elms, gums, and other trees different from those in the better-drained areas. Each of these fairly uniform areas is considered by the ecologists as the biological unit of natural areas and is called a community. Each community has a definite set of animal species living in it, a set that persists year after year with only minor change. The animal species living in similar communities are practically the same. Thus oak–hickory communities in Wisconsin, Indiana, Missouri, and Oklahoma are each populated by very nearly the same species of animals.

Although an elm or gum forest community contains a fair proportion of the species found in an oak–hickory community, it lacks many species found there but possesses in addition species distinctive to itself. If we go further afield, a prairie community has a species make-up differing greatly from that of a forest community, and both have almost nothing in common with aquatic communities.

Examining communities more closely, we see that the animal species in each are stratified in various ways. In terrestrial communities some of the animals live in the soil, some on the herbs, and some in the trees, if the habitat is a forest. There is a vital relationship between various organisms in the community, as between herbivorous animals and the plants they eat, or between predatory animals and their prey. Altogether these coordinated relations make a network of dependency that binds all the diverse individuals of a community into a biological whole.

There are two ways of looking at these phenomena. One is from the standpoint of the community as a whole, studying its development, population, the interrelationships of its component species, and the distribution of the kinds of communities over the face of the earth. Study from this viewpoint is *synecology*. The other way is from the standpoint of individual species involved, to find out in what communities they are distributed, what niches they occupy, and why. This study is *autecology*. Synecology and autecology together are the broader field of ecology, which may be defined as the study of the relations between living organisms and their environment. A treatment of ecology as a whole is beyond the aim of this book. There is, however, a great deal of important information about insects in relation to their environment that can best be organized according to ecological factors. This material having a direct bearing on insects is dealt with in this chapter. Ecological considerations are becoming of increasing importance in insect studies and are giving valuable aid to taxonomy, zoogeography, and insect control.

AUTECOLOGY

Each insect species is specially adapted to live in a particular "niche" in the community. In a sense, the species is a prisoner in its abode, because there are various environmental factors such as climate and food that restrict the species to its type and habitat. The limits of these factors within which the species can exist are spoken of as its ecological tolerance, which varies for different species in regard to the several factors involved. Correlated with its ecological tolerance, the individuals of a species have instinctive reactions which tend to insure that they will always move to the place of optimum conditions afforded by the community for their success.

Ecological information about the species falls into two main divisions: environmental factors, that determine where the species may live, and instinctive reactions or tropisms, that enable the insects to find and stay in the conditions best suited for the species.

Environmental Factors

The most important environmental factors concerning the distribution and abundance of insects are climate, physical and chemical conditions of the medium, food, enemies, and competition.

Climate

The climate forms a blanket over the entire community and directly or indirectly affects conditions and organisms in practically all parts of the community. Climate is a composite condition of which light, temperature, relative humidity, precipitation, and wind are the most important ecological components.

Light. Little definite information is available concerning the ecological effect of wavelengths making up the greater part of sunlight (ultraviolet to red). In most experimental work on the subject there is considerable doubt if light is the only variant factor involved. A great number of insects normally diurnal in habit have been reared successfully for many generations either in artificial light deficient in many wavelengths or in total darkness. It would appear, therefore, that the effect of light on most insects is indirect and expressed through quality of food caused by plant reactions to light. Light, however, is an extremely important factor in insect behavior and is considered in this relation in the section on tropisms.

Temperature. In the lives of insects temperature is one of the most critical factors. Insects are cold-blooded, so that within narrow limits their body temperatures are the same as that of the surrounding medium. Except for a few unusual instances, insects are unable to control the temperature of their medium; instead they have physiological adjustments that enable each species to survive temperature extremes normally occurring in its ecological niche (see p. 139).

The honeybee is the best-studied example of an insect that regulates the temperature of its surrounding medium, in this case, the air within the hive. In summer the hive is maintained at about 95°F. If the temperature rises above this point, bees at the hive entrance set up ventilating currents by fanning their wings, and other bees may bring water and put it on the comb to obtain the cooling effect of its evaporation. In winter the bees keep the hive up to a safe temperature by heat obtained through oxidation of foods in the insects' bodies. When the hive temperature goes down to 55°F., the bees are stimulated to muscular activity, consuming more food and liberating more heat. This continues until the temperature in the hive reaches about 95°F., when the bees become quiescent again. The temperature then gradually drops until it reaches 55°F., and the cycle is repeated. This series of cycles, called Lammert's cycles, continues all winter, each cycle lasting about 22 hours. Other social bees and ants exercise a certain amount of control over nest temperatures.

Effects of temperature are shown in two ways, the effect on rate of development, and the effect on mortality.

Effect on Development. Because they are cold blooded and their body temperature reflects that of their medium, the temperature of insects is not constant. The chemical reactions of metabolism therefore automatically speed up with an increase in temperature. As a result we find that temperature has a marked effect on insect development and activities. Now all chemical reactions do not respond at the same rate to temperature increase, and certain physical factors, such as the solubility of gases in liquids, tend to produce unfavorable metabolic conditions as temperature increases. As a result, insect development is not equally responsive to changes over the entire temperature scale. There is a definite low point at which development stops, called the threshold temperature; this point may be 10° to 50° above the actual point of death from low temperature. There is also a definite high point for each species at which development stops; this point is usually very close to that of lethal high temperature.

Between these two points, rate of development responds to temperature changes. But the response is not uniform throughout the insect world. Each species has its own individual rate of development. Figure 398 illustrates differences in rate of development for four species of grasshoppers. Within a species each developmental stage may have a different rate of development. This is well illustrated by the various stages of the Japanese beetle as graphed in fig. 399. The eggs and pupae have a much higher rate than do the larval stages, at identical temperatures.

An interesting example of dissimilar developmental rate is shown by eggs and nymphs of the red-legged grasshopper. The rates of

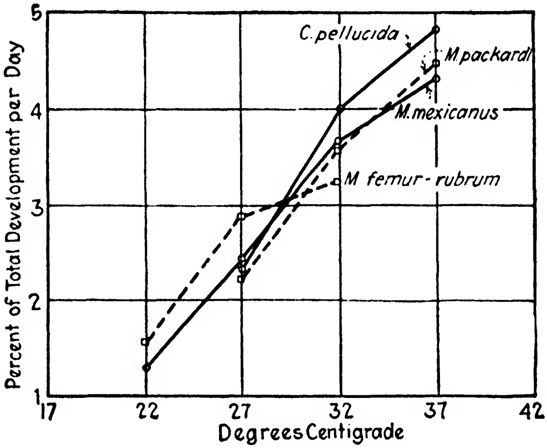

FIG. 398. Rates of development of four species of grasshoppers at constant temperatures from 22° to 37°C. (= 71° to 98°F.). (After Chapman, "Animal Ecology," by permission of McGraw-Hill Book Co.)

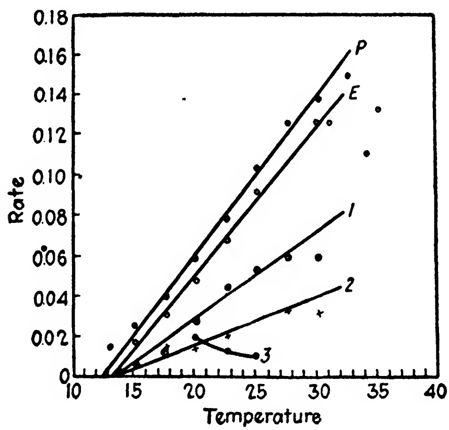

FIG. 399. Comparison of the rates of development of each stage of the Japanese beetle. Temperature scale in centigrade, 10° to 40°C. (=12° to 104°F.). (After Chapman, "Animal Ecology," by permission of McGraw-Hill Book Co.)

development for eggs and nymphs are extremely different from each other. For the nymphs the developmental rate increases steadily with increase in temperature to a point close to the lethal high temperature. The rate for the eggs increases with the lower range of increased temperature and then decreases with additional temperature increase. With the eggs this point of decreased development is reached far below the lethal temperature.

These cases show the necessity of studying separately the various stages of the life history in order to obtain accurate information on the developmental phase of the species.

Seasonal Coordination. The different rates of growth of species feeding on plants or cold-blooded animals are correlated extremely closely with the growth rate of their hosts. The result achieved is that, when the host has reached a point favorable for a certain insect to attack it, that insect has reached the proper stage to make the attack. Let us examine this relation in two species of Hymenoptera, a sawfly (Tenthredinidae) and its ichneumonid wasp parasite (Ichneumonidae). The sawfly adults emerge first early in spring at a time when the host plants have young leaves suitable for oviposition. The eggs hatch 1 or 2 weeks later when the plant is in the midst of vigorous growth and is providing a bountiful supply of food for the larvae. The ichneumon wasp has either a slower development or one that starts at a higher temperature, so that the adult ichneumonid emerges about 3 or 4 weeks after the adult sawfly. At this time the sawfly larva is nearly full grown and at the right stage for the ichneumon adult to lay eggs on it.

Another example is a group of aphids or plant lice (Aphididae) feeding in the spring on apple. The developmental rate of the overwintering eggs is such that the young aphids hatch at almost the exact time the apple buds first begin to open in spring. The aphids feed immediately on the minute leaves of the opening buds.

So constant is this coincidence of certain insect events with definite plant events that the plant phenomena (which are easy to see) are used as guides in many control programs. There are "bud sprays" for early aphid control, "petal-fall sprays," "calyx sprays," and so on, in which plant development is taken as a criterion for insect development.

Effect on Mortality. The temperature range that insects can withstand varies tremendously with the species. The most heat-resistant insects known die at temperatures of 118° to 125°F. Probably the great majority have a high lethal point from 100° to 110°F. Species that live in cool places have correspondingly lower heat tolerances, such as the mountain genus *Grylloblatta.* The optimum for this group is about 38°F., and normal activity occurs between the approximate range 30 to 60°F.; heat prostration occurs at about 82°F.

Temperatures low enough to cause death vary as much as lethal high temperatures. Insects of tropical origin usually succumb as the temperature drops near freezing, fig. 400. The confused flour beetle, for example, will die in a few weeks at 44°F. Many insects die at temperatures only a few degrees below 32°F. (0°C.). Hibernating stages

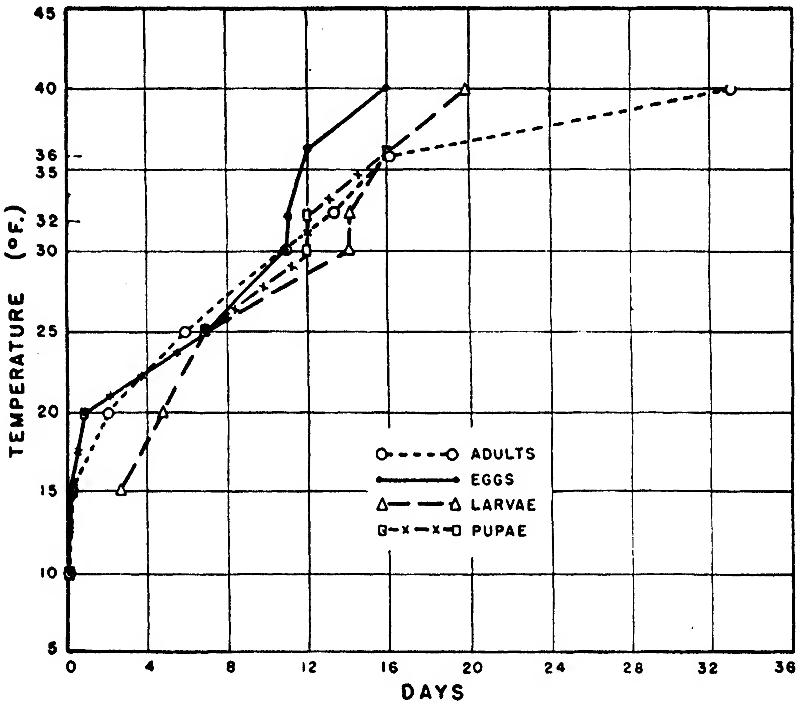

FIG. 400. Days of exposure required for assuring complete mortality of eggs, larvae, pupae, and adults of the cigarette beetle at various temperatures ranging from 15° to 40° F. (After Swingle)

of most northern insects are remarkably resistant to cold. The hibernating pupa of the promethea moth, for example, can survive continued exposure to −31°F., and some other insects are known to survive −58°F.

Insects occurring in regions having freezing winters almost invariably exhibit a different temperature tolerance in each stage of their life cycles. At least one stage is resistant to low temperatures, and in this stage the species is able to withstand the winter temperatures (see p. 141). Parasites of warm-blooded animals are exceptions. The resistant form may be the egg, nymph, larva, pupa, or adult. In most cases only a single stage is cold-resistant; when winter arrives, the resistant form lives, and individuals in any other condition die. Thus in chinch bugs only the adults are cold-resistant; when extremely low winter temperatures occur, the adults live, and any nymphs still remaining in the field die.

In their natural environment insects are well adjusted to prevailing usual temperatures. It is in the unusual seasons of hot or cold weather that temperature operates as a restricting factor. An unusual hot period will kill off the individuals of a species along the southern portion of its range, or an unusual cold period will reduce the population along the northern portion of its range. The southern house mosquito *Culex quinquefasciatus* often migrates northward and extends its range during mild winters, but is cut back southward during severe winters. The general action of unusual extremes of temperature is to modify or control the range of species along some frontier. The effects of high temperatures are usually cooperative with humidity or other factors.

Unseasonable temperatures, such as early or late frosts, may be as effective as temperature extremes in this action, because unfavorable conditions may occur before a species has entered the stage at which it is immune to them, or after it has passed to a susceptible stage. For instance, in the north-central states hibernating chinch bugs cannot withstand many alternate periods of freezing and thawing. A winter that has a number of unusual warm thawing periods, each followed by a zero or subzero period, produces this alternation of freezing and thawing and is extremely destructive to chinch-bug populations. Unfavorable temperature conditions of this unseasonable type occur hit-and-miss anywhere over the range of the species and affect peripheral areas of the range only accidentally. Their effect, therefore, is to reduce the species population in local or regional areas, in other words, to control abundance within the range rather than control the outline of the range itself.

Humidity and Evaporation. It is difficult to separate the factors of humidity and evaporation in their effect on insects, either experimentally or zoogeographically. Humidity pertains to the amount of moisture in the air, and evaporation to the actual water loss of a surface. In experimental work, if insects are subjected to low humidities, the evaporation from their bodies increases. Because of their small size, increased evaporation quickly depletes the water content of insects' bodies. In prolonged experiments, to test the effect of humidity it is therefore necessary to allow the insects to replenish their water supply by feeding. Unless this precaution is taken, effects due to desiccation may be attributed to humidity conditions of the medium. The graph in fig. 401 delineates the relation between evaporation and humidity for a common grasshopper under conditions of starvation.

There is little conclusive evidence available for making generaliza-

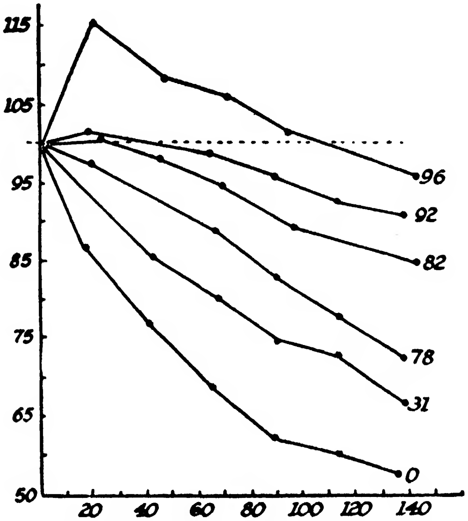

FIG. 401. Rate of loss of weight in *Chortophaga viridifasciata* at different relative humidities indicated at the end of each curve. Vertical figures represent weight as percentage of original weight, horizontal figures indicate time in hours. (From Wigglesworth, after Ludwig)

tions regarding the effect of humidity on insects. Much more work is needed before this can be done. Available data indicate that, in general, humidity is not so critical a factor as is temperature, but that each species has an optimum, which may be different for various stages of the life cycle. In the bean weevil the larvae develop faster at high humidities, but the eggs and pupae develop more rapidly at low humidities. In many cases, however, the rate of growth has been found to be practically constant over a wide range of humidity conditions.

Humidity also affects mortality rate. Low humidity has been found to increase mortality of *Drosophila,* and high humidities are recorded as interfering with hatching and molting in some species of aphids. In certain cases it has been found that high humidities apparently reduce the resistance of a species to fungus attack and act unfavorably to the insect in this manner.

There seems little doubt that humidity and evaporation constitute the barrier that restricts the geographic range of many species of insects along some periphery. There are many species occurring in eastern North America whose range extends westward to about the Mississippi River. The less humid conditions to the west appear to

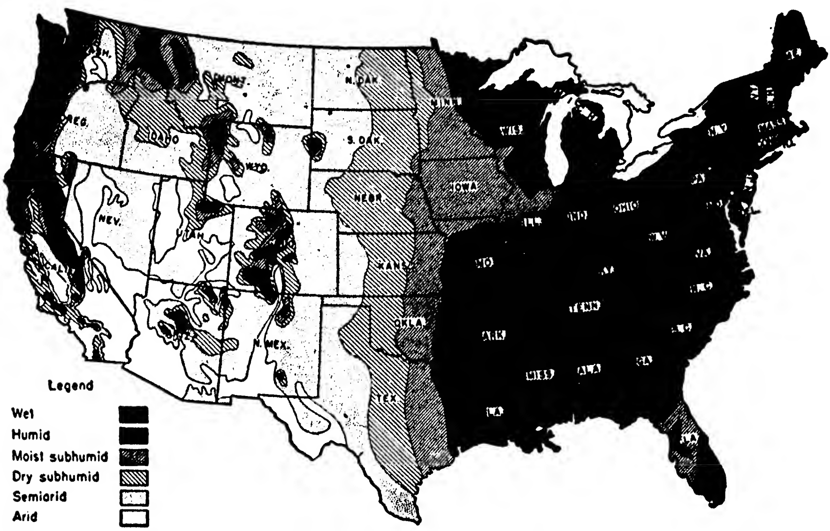

Fig. 402. Climatic moisture bands in the United States. (Adapted from U.S.D.A.)

be the factor that prevents further extensive spread of these species in that direction. Conversely, there are other species occurring in the Great Plains area which do not extend much further eastward, probably because their optimum humidity requirements are lower than those of eastern species. The assumption that humidity is the limiting factor in these cases is based on the fact that, in general, lines of equal rainfall go from north to south in the area east of the Rocky Mountains, the heavy rainfall bands occurring to the east, and the scant rainfall bands to the west, fig. 402.

Temperature and Humidity. Together these two have a marked effect on both general development and distribution of insect species. Their action is frequently critical on different phases of a species and at different times of the year. Critical cold temperatures, for instance, might operate in winter against the hibernating mature larvae, whereas adverse humidities might operate during the summer against eggs or actively feeding larvae.

Daily Rhythm. During the 24-hour cycle of day and night there is a daily rhythm of temperature and humidity characteristic of each area. Except during diapause activities of most insects are correlated very definitely with this rhythm. The most conspicuous example of this is found in areas having hot days. During the heat of a summer day, when the humidity is depressed, many insects will be relatively inactive, frequenting cooler and moister niches. Toward dusk there is a drop in temperature and a sudden increase in humidity. During this period a great number of insects emerge from daytime hiding and swarm over the ground and foliage, and in the air.

Air Movement. Insofar as physiological effects are concerned, air movement has little direct action. As wind it acts indirectly by influencing evaporation and humidity, and by causing evaporation it is an aid in reducing temperature.

As a physical force it plays a remarkable role in insect dissemination. The upward drafts caused by dawn and dusk air-convection currents carry an astonishing diversity of insects hundreds of feet in the air. Insects caught up by these currents include not only a large array of winged insects but also small wingless forms such as springtails (Collembola). It is principally on this group of air-borne insects that the swifts and nighthawks feed.

Many cases are on record of strong-winged insects such as the *Erebus* moth being blown by storms a thousand miles or more north from their tropical homes. Occasional specimens of the *Erebus* moth have been found, still alive, in Canada, the end of a journey started in Mexico, the West Indies, or southward. Shorter wind dispersals of large numbers of butterflies and moths are fairly common.

One of the most unusual wind-dispersal phenomena in the insect fauna seems to be that of the potato or bean leafhopper *Empoasca fabae.* In the United States this little insect apparently hibernates only south of the frost line. In spring it builds up huge populations in the southern states, and, later, clouds of the adults are blown northward and dispersed throughout the central and northern states, where they multiply during the summer. According to available information, winter kills off the northern populations, and each year the entire northern area of this insect's summer range is repopulated by wind-borne migrations from the south.

Physical and Chemical Conditions of the Medium

The medium in which insects live may either temper or accentuate factors of the climate and, in addition, impose definite conditions peculiar to itself on the organisms living within it. From a practical standpoint, three media are of paramount importance: terrestrial, subterranean, and aquatic.

Terrestrial Medium. For the purposes of this discussion, the terrestrial medium is considered as the surface of the earth and everything above it. This includes the aerial and arboreal regions, but it is difficult to draw a satisfactory line between these, because so many insects move frequently and rapidly from one to another.

In the case of free-living insects, conditions of the terrestrial medium are essentially those of the climate. Differences from it depend on cover. In desert and grassland areas the temperature of the medium is the sun temperature rather than the shade temperature (which is official climatic temperature). In forested areas the shade temperature prevails, and the humidity is maintained at a higher level than in adjacent open country.

Microhabitats of various types have peculiar conditions. Rotting organic matter produces heat of fermentation that adds to the temperature. Insects in fungi, plant galls, leaf mines, and tunnels in living trees enjoy a high humidity that approaches an aquatic environment. Insects in rotten logs find a moderation of extreme temperatures due to insulation, and their medium approaches the subterranean in character.

Subterranean Medium. No insects live in rock, so that we may consider as the subterranean medium for insects only that part of the substratum that classifies as soil and sand. This medium reflects the general climate but tempers its extremes and at the same time possesses several important characteristics of its own.

Tempering of Climate. Depending on circumstances, soil acts as a sponge, an insulator, and a radiator. It stores rain, giving it up slowly, so that its humidity, or moisture content, fluctuates over a much narrower range than does that of the air. Its surface layers soak up heat and insulate the part beneath; the absorbed heat is also given up slowly, so that diurnal rhythm and temperature extremes are greatly moderated in comparison to those of the terrestrial medium.

Soil properties. Many properties of soil are characteristics of the soil itself and are not superimposed by the immediate climate. Important among these are texture, moisture, drainage, chemical composition, and physiography.

These characteristics are almost entirely a direct result of the geological history of an area and reflect the type of strata exposed, glacial action, wind-carried material, or volcanic activity. To these factors are added the accumulated effects of the vegetation over a long period of recent time. Prairie plants, for instance, have built up thick black soils in many areas; forests tend to build thinner and lighter soils.

Man's activities have disturbed natural soil conditions more than any other element of the ecological pattern. Not only does cultivation change the original condition of the soil, but also ploughing and tilling keep changing it at various intervals, drainage or irrigation decreases or increases moisture content, and methods of farming can increase or decrease chemical constituents and organic content, the latter influencing texture profoundly. These changes have been detrimental to many insect species but have allowed others to increase and become major crop pests.

Texture. Soil texture varies from hard-packed clays to loose sands. Few insects occur on the harder-packed types, since they are unable to push or dig their way through them. The loams are probably the favorite soils for insect use. These allow digging and burrowing operations and are usually favorable in other characteristics, such as moisture content, drainage, and organic content.

The critical effect of soil texture on species abundance was demonstrated by the pale western cutworm *Porozagrotes orthogonia.* A species of the northern prairies, it was a collectors' rarity in the early days of collecting in central North America. After extensive breaking of the prairie sod and cultivation of the land in northern United States and Canada, this cutworm increased sharply in numbers, and the larvae became extremely destructive to grain crops. Investigation of the cause of increase revealed this situation. The female moths insert their ovipositors into the soil and there deposit the eggs. In unbroken prairie sod the eggs could be forced down only a short distance and suffered a high mortality from desiccation. Cultivated soil is of much looser texture, so that in it eggs can be laid deeper, to the full length of the female abdomen and ovipositor. At this greater depth the eggs are in a more moist layer of soil and suffer little loss from desiccation.

Drainage and Moisture. The moisture content of the soil is affected greatly by drainage. Impervious layers of substrata, such as clay or rock, may retard natural drainage, resulting in permanent or temporary semimarsh conditions or wet soils. In such situations occur only those insects that are at least partially modified for aquatic existence, such as many larvae of Diptera. In other cases impervious substrata may cause the water to percolate a considerable distance underground and, as seepage water, affect moisture conditions in other areas.

More open types of subsoil, such as sand, gravel, or shale, allow free drainage, contributing to the maintenance of better-aerated soils and more rapid restoration of normal moisture content after rains. Well-aerated soil is a prerequisite of all soil insects that have no modifications for aquatic or semiaquatic existence.

An interesting demonstration of the effect of soil moisture on an insect species is the case of the Colorado corn rootworm *Diabrotica virgifera*. Collecting records indicate that until recent years this species was a fairly rare one occurring in the arid regions of New Mexico, Colorado, and Nebraska. The larvae feed on corn roots and, if present in large numbers, may destroy the root system of the plant and cause great reduction in yield. Since about 1890 the species has been a constant pest in south-central Nebraska but practically disappeared during the drought years. In the last decade, however, the species has become of major importance in the irrigated portion of the Platte River valley, owing to the increase in soil moisture resulting from more widespread irrigation.

Wireworms in the Pacific Northwest afford another striking example of changes in species composition and abundance due to changes in soil moisture. In that region four species of wireworms, *Limonius californicus*, *infuscatus*, *canus*, and *subauratus*, are wet-land pests, normally restricted to swamp and river-bottom areas. When arid land was irrigated and used for farming, these wet-land wireworms became important pests of potatoes, corn, lettuce, onions, and many other crops grown in irrigated fields. The high soil moisture maintained by irrigation apparently allows the wireworms to increase in great numbers, fig. 403.

Drainage and texture together exert considerable influence on the distribution of insects that live part of their life in the soil. The range of the destructive Texas leaf-cutting ant *Atta texana* extends into Louisiana, and there the species nests only in fine sandy loams having light subsoils and excellent drainage.

Chemical Composition. Except for poisonous chemicals and organic compounds constituting food, the chemical composition of the soil influences insects indirectly, through its effect on plant growth. Plants are very responsive to chemicals in the soil, so that available chemical substances determine to a considerable degree the species of plants that are available for insect food.

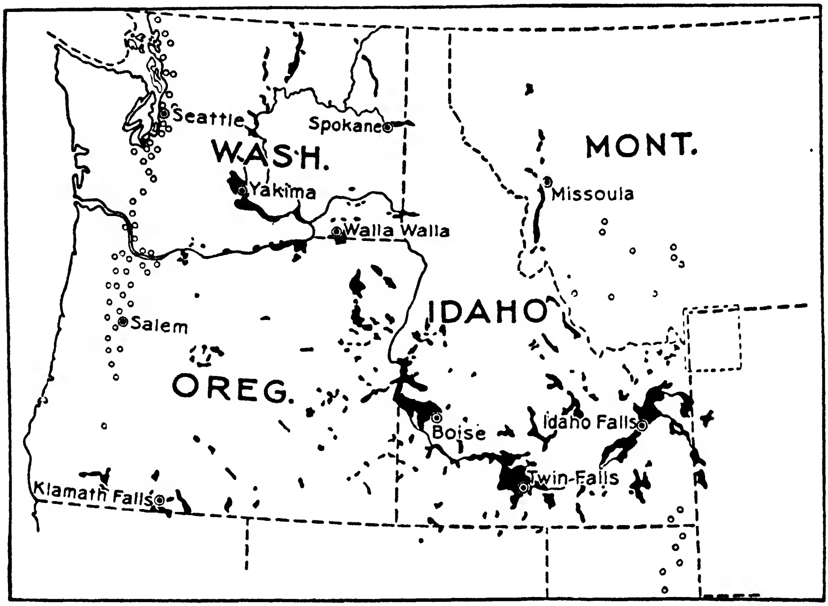

FIG. 403. Distribution of wet-land wireworms in the Pacific Northwest. Black areas represent irrigation projects on which one or more species of wireworms cause serious injury to crops annually. Circles represent places where wireworms are known to occur and cause occasional injury. (From U.S.D.A., B.E.P.Q.)

Physiography. In itself, physiography has few direct effects, but it has a marked influence on several soil factors. Flat country has slow rain runoff and must have adequate subsurface drainage to maintain good soil aeration. Hilly or mountainous country has rapid water runoff insuring good general soil aeration. In addition south, east, and west exposures have a higher soil temperature, greater evaporation, and, as a result, some differences in plant life.

Aquatic Medium. Conditions in water are obviously different from those on land or in soil. There does not exist the question of moisture and evaporation, the most critical single problem in the terrestrial medium. Instead, oxygen and respiration are the critical complementary problems of aquatic insects, and many characteristics of the aquatic medium are important because they have a direct bearing on these. In other words, for insects living in air, water is the chief problem; for those living in water, air is the problem.

Aeration. Of great importance from the standpoint of many aquatic insects are the diffusion of excess carbon dioxide out of the water and the diffusion or solution of oxygen into it. In most cases the latter is the more important. The oxygen comes from the air, and any stirring movement that brings more water into direct contact with the air increases the oxygen supply. In lakes and ponds wind action is the chief agent. Waterfalls, rapids, or movement of current are stirring agents in streams, in order of greatest efficiency.

Temperature has a direct bearing on aeration, because the colder the water, the greater is the amount of gases (including oxygen) that will dissolve in a given volume of water. High temperatures greatly decrease the solubility of gases in water.

An important distinction must be made regarding aeration among aquatic insects. Many groups, such as mosquito larvae, horsefly larvae, and certain aquatic bugs have extensile respiratory tubes that reach the surface, or the individuals periodically come to the surface to breathe; others, such as the water boatmen or adult diving beetles, take a bubble or film of air into the water with them, coming to the surface to replenish it from time to time (see p. 149). These groups are almost independent of the aeration factor in water, and many live in water almost devoid of oxygen.

Aquatic insects without modifications for obtaining direct contact with air are dependent for respiration on oxygen in the water. As with other ecological factors, various insects have different aeration requirements and are limited in distribution by it. Certain dragonfly larvae and midge larvae are examples of forms able to tolerate very poor aeration and are often found in stagnant ponds. Larvae of the midge family Blepharoceratidae have extremely high oxygen requirements and occur only in rapid mountain cascades.

Temperature. Aquatic temperatures do not have the same range as climatic temperatures, but in most bodies of water there is a definite temperature response to air conditions. Insect species usually show a definite restriction to water of a certain temperature range. In many cases this is undoubtedly correlated directly with aeration, but in some cases temperature is probably the factor. Certain mosquito larvae, for instance, live and transform normally in water at 65°F. but die during molting in water at 80°F. Since mosquitoes are not dependent on water for oxygen, it appears that in this case temperature is a factor.

A few aquatic insects have been found in hot springs with temperatures ranging from 110°F. to 120°F. These are chiefly aquatic beetles and fly larvae that obtain oxygen directly from the air.

Temperature plays the same part in relation to growth and activity in aquatic insects as in other insects, as discussed on page 448. Through adjustment to temperature, various aquatic species appear at various times throughout the year. For the most part develop-

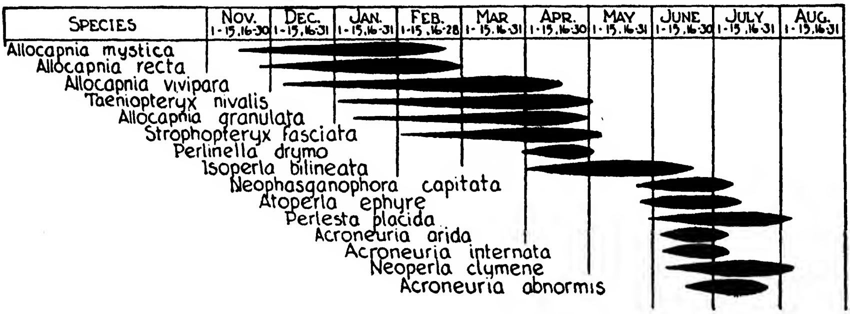

FIG. 404. Seasonal succession of adult emergence for 15 stonefly species at Oakwood, Ill. The widest part of the spindle indicates the time of maximum abundance of adults for each species. (From Illinois Natural History Survey)

ment and activity increase as water temperatures rise, resulting in the production of great swarms of adults through late spring and summer.

In the stonefly genus *Allocapnia* the reverse is true. The nymphs live in streams throughout the north-central and eastern states. During summer, nymphal growth seems to be retarded but increases with the advent of cool autumn weather. As a result the adults emerge during the winter months, beginning during late November and continuing until February or March, fig. 404.

Depth. In lakes and ponds depth has a marked influence on oxygen, temperature, and light; in running water the effect of depth is less marked owing to the stirring action of the current.

Water absorbs heat and light passing through it, converting the latter to heat. Heat rays and the red end of the light spectrum are absorbed first; at greater depths the other wavelengths are gradually absorbed until, even in very clear lake water, almost all light is absorbed at about a hundred feet. This has a profound effect on plant life. Practically none exists below the 60-foot level, and most of it is concentrated in the first 6 or 10 feet of water where there is a good supply of light for photosynthesis. This produces a zonation of food supply that in turn limits the distribution of many insects.

Depth in deep lakes (100 feet or more deep) is accompanied by another phenomenon of great biological interest, the thermocline. In summer the surface waters of a large lake are appreciably warmer than the water at the bottom, which remains near its point of greatest density, 38–40°F. (= 4–5°C.), fig. 405. This bottom layer being the

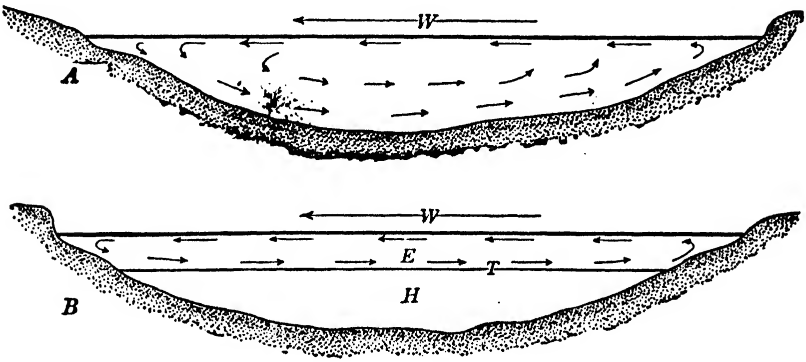

FIG. 405. Diagrams illustrating a thermocline. The circulation of the water (*A*) in a lake of equal temperature, (*B*) in a lake of unequal temperature. *W*, represents the direction of the wind; *T*, thermocline; *H*, hypolimnion. (From Ward and Whipple, after Birge)

heaviest, the upper warmer waters "float" on it, rather than mixing with it. Between the two is a relatively narrow dividing area, the *thermocline*, intermediate in general conditions between the fairly uniform upper and lower strata. The upper stratum, the *epilimnion*, is churned and agitated by wind action so that it is almost uniform in temperature and well aerated. The bottom stratum, the *hypolimnion*, is stagnant, and its oxygen is gradually used up by organic oxidation. Almost all the life in a deep lake occurs in the epilimnion; the hypolimnion is practically a biological desert.

Turbidity. Minute particles of earth or "blooms" of algae and other organisms usually cloud water to some extent. The clouding or turbidity has an indirect effect on insects, because it reduces light penetration and therefore plant production on the bottom. Under conditions of continuous high turbidity, there is persistent settling of suspended material on the bottom, thus modifying its character and its fauna.

Bottom. The great proportion of aquatic insects live on or in the bottom, and most species will live only where the bottom is of a particular type. The most useful categories for purposes of classifying the bottom types are based on size of particle: namely, muddy, sandy, and rocky. Mud bottoms are highest in organic material that serves as food; sandy bottoms and rocky bottoms have the least. Mud bottoms in streams, however, are usually associated with slow current, lower oxygen content of the water, and higher temperatures. Sandy bottoms are relatively unstable and usually have a small fauna. Rocky bottoms afford the most stable footing and are the favorite habitat for a large number of groups.

Vegetation. To some insects aquatic vegetation is primarily food; to others it is a haven. Vegetation beneath the water provides shelter and footing, especially valuable to species that are the prey of other animals or that have no special adaptation for swimming. Aquatic vegetation is especially abundant in lakes, and it is there that it is most useful. Relatively few lake-inhabiting insects frequent open water; they stay on the bottom and in the weed beds most of the time. Those that move about freely in the open water usually do so only at dusk or night, hiding on the bottom during the daytime.

Food

Food is one of the most important factors influencing the distribution and abundance of insects. For many insect species it is a factor that has been changed radically by man's agriculture, travel, and transportation.

As a Factor in Distribution. Often the range of the host plant for a given species of insects extends much beyond that of the insect, demonstrating that some other factor such as temperature or soil conditions is the actual factor limiting the insect's success and distribution. In other cases it is obvious that the insect is usually present wherever a suitable food is present and is prevented from extending its range because of the food factor. This is graphically shown in the case of many plant lice that have become successfully established on agricultural crops far beyond the range of the native hosts of the insects.

General Feeders. Many insects have a wide assortment of acceptable hosts or prey or feed on material such as decayed or dead organic matter that is widely distributed through most biotic communities. In these food is only infrequently a limiting factor of distribution. Areas in which such species are absent usually have food material, but other factors such as temperature or moisture may be intolerable for the species.

Specific Feeders. A great number of insect species, including chiefly plant feeders and parasites, feed on only a small number of diverse host species, or are restricted to a group of closely related host species, or may be restricted to a single host species. All intermediate conditions of host specificity or tolerance occur between these extremes. The species that have the most limited host tolerance are the ones that are most likely to have their distribution limited by food. The over-all range of the Hepatica sawfly *Pseudodineura parvula* appears to cover all of the north-central and northeastern states; yet in the north-central states the sawfly occurs only in the scattered localities in which its host, *Hepatica,* is found. The black-locust sawfly *Nematus tibialis* is normally confined by the rather restricted eastern range of its host, *Robinia pseudoacacia.* Whenever the host has been planted in other localities, the sawfly has ultimately been found, even in England, indicating that the sawfly has a much wider ecological tolerance than that indicated by the natural range of its host.

Host Crossover. In the case of insects feeding on a definite species of plant host, this latter may become defoliated, and it is necessary for the species to adopt a new host or to have its numbers reduced to the carrying capacity of the original host. Experimental investigations of this crossover of an insect from one host to another have brought out some exceedingly interesting information:

1. Some species, such as the forest tent caterpillar, make the change to closely related hosts with ease and without evident ill effects. Chinch bugs, for instance, will feed on oats or wheat until nearly full grown and can transfer to corn readily and without noticeable mortality due to food reactions.

2. Other species will make a change from one host to a close relative with the greatest difficulty, either after compulsion of a period of starvation (in the case of immature stages) or under circumstances of extreme necessity (in the case of ovipositing females). In most cases of this kind the transfer cannot be made by advanced larvae. They will eat the new food but develop symptoms of intestinal disturbance, such as diarrhea, and die. If first-instar larvae are put on the new host, they will eat but suffer an extremely high mortality. During succeeding instars the mortality rate decreases until the pupal stage is reached, and here the mortality is again high. But out of

thousands of first-instar larvae a few adults will finally be obtained. These will prefer to oviposit on the new host, and the resulting larvae will feed on it readily and without ill effects.

An interesting case of this type was supplied by the satin moth *Stilpnotia salicis*. A European pest of Lombardy poplar, it was introduced on the Pacific Coast about 1922 and in a few years became very abundant, completely defoliating Lombardy and other introduced poplars in each locality to which it spread. In British Columbia by the late 1920's it had spread up the valley of the Lower Fraser River. There it built up a large population and practically exterminated the Lombardy poplars in that region. When Lombardy poplars were no longer available, the satin moths began laying eggs on the native cottonwood *Populus trichocarpa hastata,* an abundant tree in this region. At first only sporadic colonies became established on this new host which is also a member of the poplar genus, but in a few years the satin moth was the most serious insect enemy of cottonwood in this area. Laboratory rearings demonstrated that in making this host crossover the satin moth went through the initial high mortality process just described.

An example of a species that does not follow this behavior is the gypsy moth *Porthetria dispar.* The gypsy moth larvae are plant feeders and will feed on over four hundred and fifty species of plants. Of these forty-two are favored hosts, including willows, birches, and oaks; later instars of the larvae may switch to one of the other four hundred and fifty host species, one of the favorites being white pine. They suffer no ill effects and develop to maturity. For normal development, however, it is necessary for the first two larval instars to feed on one of the forty-two favored species.

The complete host relationships of only a relatively small number of insect species have been studied comprehensively. Undoubtedly much interesting material will continue to be discovered on this subject.

3. A third group of species appear to be tied irrevocably to a single species of host. If put on even a closely related species, they will die before they will feed, or all die if they do feed.

These phenomena of host crossover have a great effect on the distribution and abundance of the insects involved and represent an important type of ecological tolerance insofar as food is concerned. They may be of economic importance if crossover cases involve agricultural species. There is always the possibility of this happening when new plants are brought into the national agricultural economy, as, for instance, the soy bean.

As a Factor in Abundance. Amount of available food is an important factor affecting the population of a species in a given community. It is not uncommon for a species to utilize its entire available food supply with a resulting sharp reduction in population due to starvation.

Although there may be considerable variation in size between different individuals of the same species, there seems to be a definite minimum amount of food required for the normal development of an individual. Housefly maggots, for instance, die during pupation if the larvae are removed prematurely from their food supply. Most sawfly larvae will die without further development if removed from their food only two or three feedings prior to completing their full food intake. If, therefore, an excessive number of individuals are feeding on an insufficient amount of food, those with a head start complete their normal food intake and mature, and many of the remainder run out of food and fail to develop.

The most notable exceptions to this are found in certain parasitic species having a wide range of hosts. In these, the size of the individual parasite is determined by the size of the respective host species. An excellent example of this is the mutillid wasp *Dasymutilla bioculata;* larvae feeding on small prey species develop into small individuals, those feeding on large prey species develop into large individuals, fig. 406.

Agriculture has changed the insect food factor in several ways: (1) by providing suitable food when or where it would not be present under natural conditions, (2) by providing better food, and (3) by simply providing a greater food supply.

Extension of Food Supply. A striking example of this factor came to light in the extensive sampling of grain in granaries in the late 1930's and early '40's. It was discovered that in many states, especially in the corn belt, a tenebrionid beetle *Cynaeus angustus* had become extremely abundant and widespread and had developed into a major pest of stored grain. This beetle was first described in 1852 from California and prior to 1938 remained a collector's rarity. It was known to occur at the base of yucca plants. In 1938 the beetle was encountered as a stored-grain pest in Washington, Kansas, and Iowa. By 1941 it was known to be widely distributed through the corn belt. The species reached population peaks in the man-made conditions of grain storage which are in astonishing contrast to the scarcity of the species in its natural habitat.

Better Food. It has been shown in some cases that certain introduced agricultural crops increased the fecundity and thereby the abundance of native insect species. The two grasshoppers, *Melanoplus differentialis* and *M. bivittatus,* showed marked increases in fecundity on a diet of soy beans and alfalfa, respectively. This is correlated with field observations of the increase in population of the two species following the planting of large acreages of the two crops mentioned.

Additional Host Material. Practically every crop favors at least a few insects in supplying more food. The Colorado potato beetle,

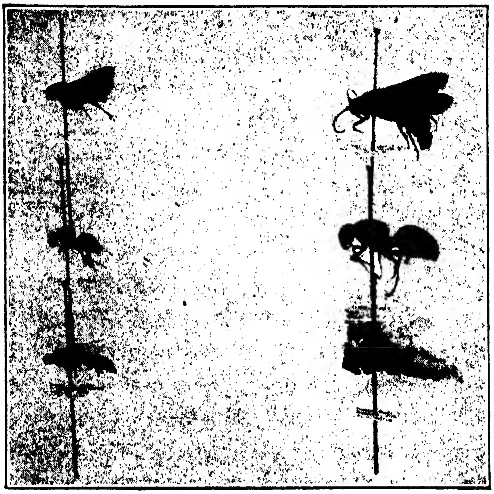

FIG. 406. Correlation in size between *Dasymutilla bioculata* and its hosts *Microbembix monodonta* (left) and *Bembix pruinosa* (right). Each vertical row has *Dasymutilla* male and female above, host wasp at bottom. (From Chapman after Mickel)

the corn aphids, and other pests on potatoes and corn certainly have flourished on the thousands of acres of host crops that man has planted and have built up huge populations that dwarf the scattered colonies that existed before agriculture, when their hosts were relatively sparse and the individual plants not so luxuriant as those of improved agricultural varieties.

Enemies

A wide array of organisms prey on or parasitize insects. Some of the parasites, such as the malarial organisms *Plasmodium* sp., seem to do the insect no harm, but the majority have a harmful effect on the insect host. These enemies constitute an environmental factor having a definite effect on the abundance, and sometimes the distribution, of the host species. Each stage of the host species may be subject to attack by a different set of enemies, or several stages may be attacked by the same one. As a rule, predaceous enemies and plant enemies such as fungi are more general in their attack on various stages, and internal parasites are restricted regarding the stage they attack.

Internal Parasites. Insects are attacked by several groups of internal parasites, of which the most important are certain groups of insects, parasitic worms, bacteria, and fungi. Other groups also parasitize insects.

Insects. The larvae of many families of Hymenoptera (Ichneumonidae, Chalcididae, Scelionidae, and many others) and a few families of Diptera (Pyrgotidae, Tachinidae) are entirely endoparasitic on insects or closely allied arthropods. A few Lepidoptera have endoparasitic larvae, and several Coleoptera, including the entire small suborder Strepsiptera, or stylopids. On the basis of rough estimates there are about eleven thousand species of parasitic insects known at present in North America. Most of these are fairly specific at least as to what group they attack. Some, for instance, will attack a wide variety of lepidopterous caterpillars; others will attack only certain primary parasites in these caterpillars (see p. 322).

Other Animals. Some species of Protozoa and invertebrate metazoan parasites pass one stage of their life cycles in insects. Examples of such protozoan parasites are the malarial organisms *Plasmodium* sp. and sleeping-sickness organisms *Trypanosoma* sp. Among the parasitic worms that spend part of their life cycle in insects are trematodes, nematodes (for example, *Filaria*), and Acanthocephala (for example, *Macracanthorhynchus hirudinaceus* the thorny-headed worm of swine). In each case only one the early stages of development is passed in the insect, which is an intermediate host for the parasite. This group of parasites does not appear to have a deleterious effect on the insect, at least not the fatal effect of the insectan parasites. It is probable, therefore, that this class of non-insectan parasites is a negligible factor in relation to insect populations.

Fungi and Bacteria. Many species of these groups attack insects in various stages and at times are destructive to their hosts. Anyone who has carried on rearing experiments with insects can well attest this, for cultures are very susceptible to attack by fungous and bacterial organisms. The reason for this is that the best development of both types of these parasitic organisms is attained under conditions of relatively high humidity and temperature which are frequently increased to an unnatural degree in caged experiments.

Among common fungus diseases of insects is *Empusa muscae* the housefly fungus, fig. 407. Other members of the same genus attack a large variety of insects, including grasshoppers, aphids, and chinch bugs. A famous fungus disease is *Beauveria globulifera,* often referred to as *Sporotrichum globulifera,* the white fungus of the chinch bug.

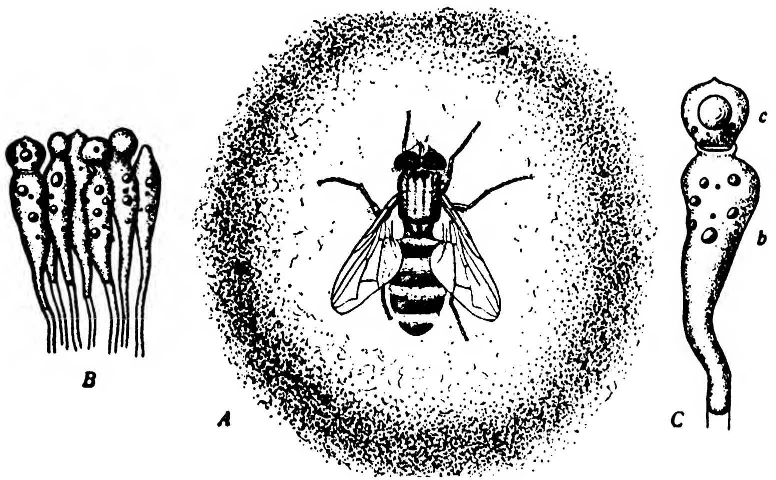

FIG. 407. *Empusa muscae* the common fly fungus. *A,* housefly (*Musca domestica*), surrounded by fungus spores (conidia); *B,* group of conidia in several stages of development; *C,* basidium (*b*) bearing conidium (*c*) before discharge. (From Folsom and Wardle, "Entomology," by permission of P. Blakiston's Son & Co.)

During warm and humid seasons this fungus kills large numbers of chinch bugs and other insects in late spring and early summer and at times has controlled the bugs to the point of local extermination. Entomophagous fungi of the genus *Isaria* are the chief species attacking insects under artificial conditions.

Of unusual interest is the fungus family Laboulbenaceae. Most of the species are entomophagous and produce elongate or ornate fruiting structures outside the body of the host insect. A species occasionally encountered in the eastern states is *Cordyceps ravenelii,* a parasite of white grubs, fig. 408.

Bacterial diseases are less numerous than fungi in species but at times are strikingly devastating. Flacherie, an infectious and highly fatal disease of silkworms, is caused by a bacterium. Grasshoppers and chinch bugs are attacked by similar bacteria, but attempts to control these insect pests by propagating and disseminating the disease have failed. Greater success has been achieved with *Bacillus popilliae,* the organism causing a disease of Japanese-beetle larvae called milky disease. The bacterial spores are mixed with an inert dust and the mixture applied on top of the soil in grub-infested areas. Rain washes the spores into the ground and into contact with the grubs. This control method has proved sufficiently satisfactory to be used on extensive areas.

External Parasites. Insects have few ectoparasites of the type of the lice or fleas, in which the adult stage or both immature and adult stage use the body of the host as a home. A few mites infest various insects, but only scant information is known regarding the ecological significance of the groups. An unusual ectoparasite is the bee louse *Braula caeca,* a curious minute fly that is ectoparasitic in the adult stage on honeybees.

In the Hymenoptera, some families whose larvae are mostly endoparasites, such as the Braconidae, contain genera whose larvae are attached externally to their host larvae. These parasites have the same host relation as their endoparasitic allies, in that normally only one parasite individual lives on one host individual, the latter almost always dying when or before the parasite is mature.

FIG. 408. Fruiting structures of a fungus *Cordyceps ravenelii,* arising from the body of a white grub *Lachnosterna.* (After Riley)

Predators. As in the case of internal parasites, so in this category too insects are their own worst enemies. Carabidae and Staphylinidae are two very large beetle families that feed in both adult and larval stages almost exclusively as predators on other insects. Many families of wasps are predaceous, as are larvae of Tabanidae, Dolichopodidae, and some other large families of Diptera. Odonata (damselflies and dragonflies) are predaceous as both nymphs and adults. The same is true of certain families of Hemiptera such as Pentatomidae (stink bugs), Reduviidae (assassin bugs), and Phymatidae (ambush bugs); in some other families of Hemiptera, such as the Miridae (plant bugs), most genera are phytophagous, but some are predaceous. There are many other small groups of predaceous forms.

Non-insectan predators of insects include members of several large groups. Spiders are primarily insectivorous; there are about three thousand species of spiders in North America, and each spider population takes its toll of insects. Centipedes feed on insects to a large extent also.

Vertebrates contain many groups that are insectivorous. Among the fish, perch, sunfish, crappies, bass, and sheepshead use insects for a large share of their diet. Reptiles and amphibians are largely insectivorous, as are bats and moles; other mammals such as mice, skunks, shrews, and raccoons eat large numbers of insects.

Birds are the outstanding vertebrate insect eaters. Swifts, nighthawks, and flycatchers feed entirely on insects caught on the wing. Robins, wrens, chickadees, cuckoos, quail, and prairie chickens live almost entirely on insects when the latter are abundant. During insect outbreaks many birds of omnivorous food habits switch temporarily to an insect diet. Crows, blackbirds, gulls, owls, and small hawks are in this group and have been noted especially feeding on grasshoppers during periods of abundance.

All these animals are abundant and, being comparatively large individuals, eat proportionately large numbers of insects. In doing so they exert a steady ecological force against insect populations.

Predaceous Plants. A list of insect predators would not be complete without mention of those curious plants that trap animal prey and digest them. Bladderworts (*Utricularia*) are aquatic plants that trap small organisms in bladder-like pouches; sundews (*Drosera*) are bog plants having sticky tentacle hairs on their leaves that encompass prey; and pitcher plants (*Sarracenia*) have leaves in the shape of pitchers, partially filled with water, with stiff hairs pointing to the water; the hairs allow insects to get to the bottom of the pitcher but prevent their escape. None of these plants is sufficiently abundant to be of importance ecologically by reducing insect numbers.

Protection Against Enemies

Insects appear to have little or no protection against several groups of their enemies, notably fungi and bacteria. Against insect parasites and predators their only protection seems to be evasion; many insect stages are extremely limited in locomotion and obtain no protection by this means.

The principal group of enemies against which insects have achieved some measure of protection is the land-vertebrate group. Against this group such devices as protective resemblance, the building of protective structures, poison hairs, bites, stings, noxious secretions, and the mimicking of species possessing some of the foregoing, offer protection to some extent.

Protective Resemblance. We have all been surprised at one time or another to discover a "stick" come to life in the net, or, in examining

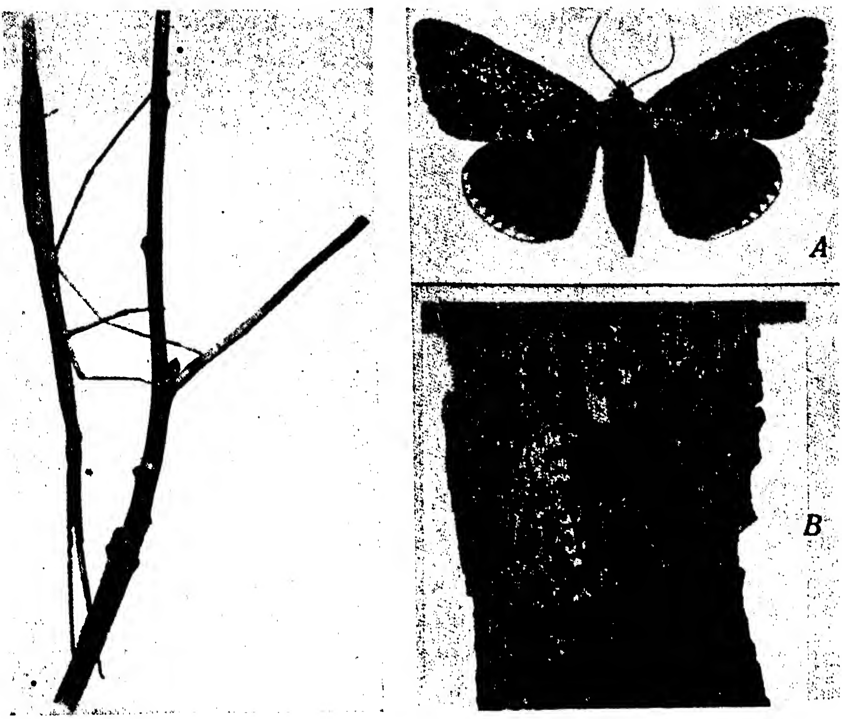

Fig. 409. Protective mimicry and coloration. At left, a walkingstick insect on a twig; at right, an underwing (*Catocala*) with wings spread (*A*) and at rest on bark (*B*). From Folsom and Wardle, "Entomology," by permission of P. Blakiston's Son & Co.)

a tree trunk, to see what appeared to be a section of bark take wings and fly away. This protective resemblance is common in several insect groups. The walkingstick insects (Phasmidae), fig. 409, resemble sticks; in spring they are green; then when mature in autumn many become brown, resembling the color of the foliage or twigs on which they feed and rest. Many moths at rest resemble bark. Some of the larger forms are the underwing or Catocala moths, perfect bark mimics with wings folded, but often conspicuous in flight owing to brightly colored underwings, fig. 409. Grasshoppers resemble lichens, various types of soil, dried leaves, or grass, depending on the species and its food. Psocids have similar protective color patterns, especially those that feed on algae or lichens on bark or rock bluffs. A few larvae at rest curl up and resemble a fresh bird dropping, notably the

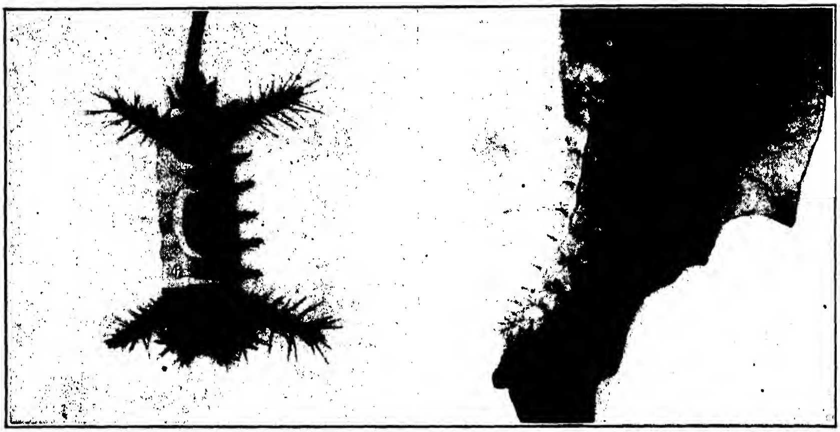

FIG. 410. Caterpillars having nettling hairs annoying to man. Left, the saddle-back *Sibine stimulea;* right, *Automerus io.* (From U.S.D.A., B.E.P.Q.)

sawfly *Megaxyela aviingrata.* In general most of the leaf-feeding larvae are green or are mottled so that they blend into the foliage on which they feed.

Building Protective Structures. Certain larvae build cases, houses, or canopies that give the occupant some physical protection and in addition may resemble the host or surroundings and result in protective resemblance. Bagworms (Lepidoptera), fig. 339, are a common example, and also caddisfly larvae of many kinds, fig. 329. Cases of the latter may be very difficult to see unless the insect is in motion. The larvae of several leaf-feeding beetles construct an urnlike case that is difficult to see in its natural surroundings.

Poisons, Bites, and Stings. Certain insects gain protection by inflicting pain on their assailants. Several caterpillars have sharp hairs, containing a poisonous fluid that causes a rash and extreme pain. So delicate are these hairs that one has only to brush against them lightly to feel the excruciating nettling sensation that they produce. Tussock moth larvae and eucleid moth or saddleback larvae, fig. 410, are protected by these. Other insects bite the aggressor, as, for instance, ants, Still others, such as bees and wasps, are provided with painful stings; bees use these only for protection; some wasps use these both for protection and for paralyzing prey.

Noxious Secretions. A large number of insects have mechanisms for producing and ejecting noxious smelly substances. Swallowtail but-

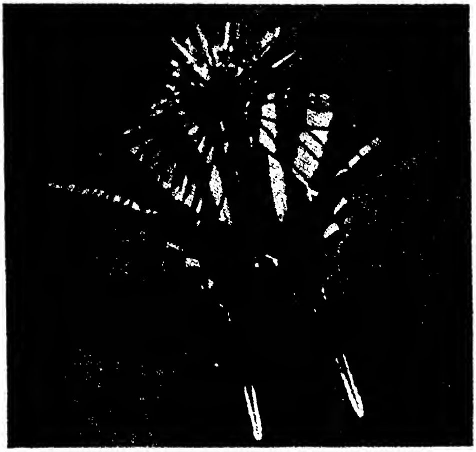

FIG. 411. A brightly colored mal-tasting butterfly *Papilio ajax*. (From Folsom and Wardle, "Entomology," by permission of P. Blakiston's Son & Co.)

terfly larvae have an eversible pair of horns, the osmeterium, on the pronotum, that give off an odor thought to be repellent to some animals. Stink bugs and many Heteroptera have stink glands on the dorsum of the abdomen. Other insects, without such definite glands, apparently have a disagreeable taste, because birds especially refuse them as food. Swallowtail butterfly and milkweed butterfly adults, and both larvae and adults of many brightly colored leaf-feeding beetles are in this category.

It is pertinent to note here that a large number of species possessing protective devices discussed in the two preceding paragraphs are strikingly marked or gaudily colored, fig. 411. This striking ornamentation may be a display of warning colors, to aid the memory of an assailant who has attacked a protected species and become aware of its defense. It is certain that birds and other vertebrates have no instincts to avoid protected species, so that each individual must learn for itself.

Fig. 412. Mimicry in bees and wasps. *Ar,* drone bee *Apis mellifera; B,* dronefly *Eristalis tenax.* (From Folsom and Wardle, "Entomology," by permission of P. Blakiston's Son & Co.)

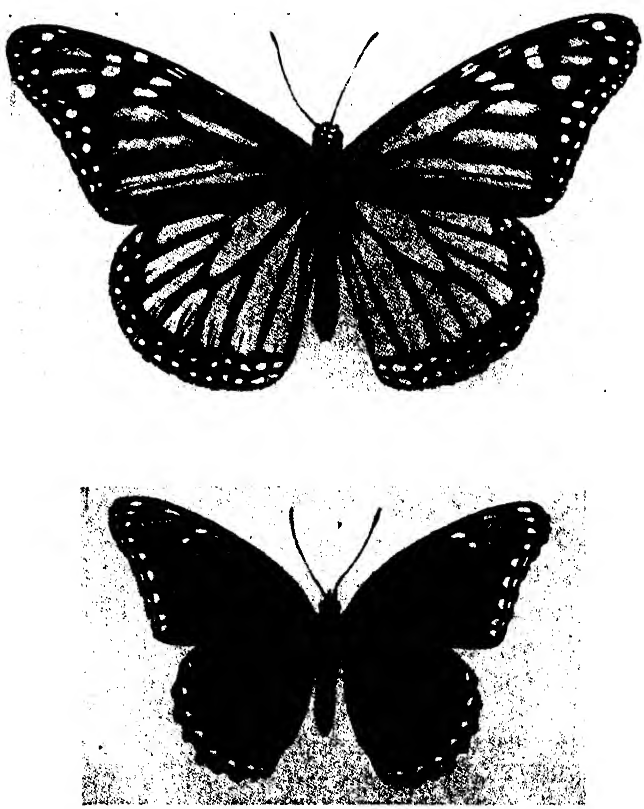

Fig. 413. The viceroy, below, and the milkweed butterfly, above. (From Folsom and Wardle, "Entomology," by permission of P. Blakiston's Son & Co.)

Protective Mimicry. Among insects having no known protective mechanism, there are some that share the protection of those that do by looking almost exactly like them. Thus there are harmless plant bugs that look like ants, harmless flies that resemble bees or wasps, fig. 412, and edible butterflies that have the appearance of distasteful species. Among our fauna the best example of the latter type, fig. 413, is the viceroy *Basilarchia archippus*, an edible species that resembles in pattern and general color the distasteful milkweed butterfly *Anosia plexippus*. In tropical faunas similar cases are common.

The advantage gained by a species through these types of protection is average, for none of these methods are absolute. Insects inedible to birds may be delectable to animals, or if refused by one kind of bird may be eaten readily by another. But, if even a small advantage is gained by a species, that species has a tremendous advantage over a long period of time.

Competition

If we suppose an individual of a species in a situation having suitable climate and conditions of medium and food, and, further, that its enemies are not a critical factor, that individual may discover another individual having similar wants is there also. If there is only sufficient food for one, then the two individuals are in vital competition from which only one can emerge as the survivor.

Among insects, competition is chiefly for food. This competition may be between either individuals of the same species or individuals of different species.

Frequently there is no reaction to critical competition, and all individuals may starve. If, for instance, sawfly larvae overpopulate a host, they feed quietly until the entire host is stripped; then all of them wander until exhaustion and death if additional food is not found. In the case of critical competition involving two or more insect species, their different requirements may mitigate in favor of one of them. An interesting example is cited by Willard and Mason (1937) regarding two hymenopterous genera *Opius* and *Tetrastichus*, that parasitize the Mediterranean fruit fly larvae in Hawaii. Within a single fruit fly larva there can develop to maturity only a single larva of a species of the braconid *Opius*, but as many as ten to thirty individuals of the minute chalcid *Tetrastichus*, fig. 414. If both oviposit in the same fruit fly larva, the *Opius* larva kills most of the *Tetrastichus* larvae, but a few of the latter escape destruction. These develop more rapidly than the *Opius* larva and reach maturity, but leave too little food for the larger braconid larva, so that the *Opius* larva invariably dies.

Competition for food is frequently active and aggressive. Pemberton and Willard (1918) give an account of such an example occurring in wasps of the genus *Opius* previously referred to. In Hawaii three

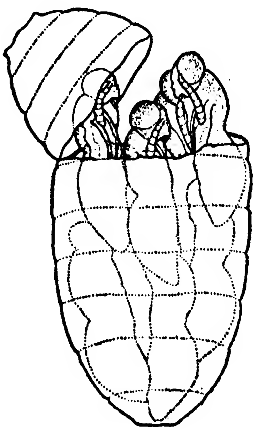

FIG. 414. Parasitic wasps *Tetrastichus giffardianus*, in puparium of fruit fly. (After Pemberton and Willard)

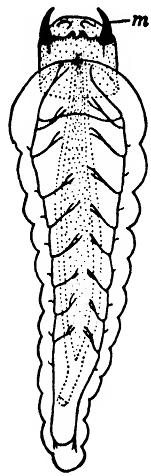

FIG. 415. First-instar larva of *Opius humilis*. Note the sharp heavily sclerotized mandibles *m*. (Redrawn from Pemberton and Willard)

species, *tryoni, fullawayi,* and *humilis,* parasitize fruit fly larvae. The female wasps lay their eggs in the fly larvae, and several individual wasps of all three species may oviposit in the same larva. Only one survives, and this one is the result of a battle among the newly hatched larvae. The first instar of each *Opius* larva has a relatively large hard head bearing a pair of long sharp mandibles that can be opened and shut with great force and speed, fig. 415. These larvae are cannibalistic and attack any other parasite larva within the fly larva, using these sharp mandibles to pierce and lacerate their antagonist's body. Whether the struggle is between individuals of the same species or of different species, only one *Opius* larva remains after the struggle is over. It was discovered that *O. tryoni* was almost invariably the victor over the other two species, owing to its greater agility, reaction time, force in use of mandibles, and other combative advantages.

Canibalistic tendencies occur in many insect groups, and are invariably accentuated by crowding. The confused flour beetle lives and feeds on a variety of stored-grain products; generations are continuous, and adults, eggs, and all stages of larvae occur together in the food. Large larvae and adults may feed on eggs and small larvae of their own species but apparently make no effort to hunt them out. When the infestation of these beetles is small in relation to the volume of their food medium, the older individuals encounter the younger stages less frequently. As the infestation increases per unit volume of food medium, these encounters are more frequent, and cannibalism increases accordingly. By this mechanism a population point is reached where the losses due to cannibalism are equal to the reproductivity of the adults, and overcrowding beyond this point is prevented.

It is pertinent to note in connection with these phenomena, that there exists no conscious sense of competition by the insect itself. The competing individuals react instinctively throughout, and these instincts under certain conditions of crowding produce the elimination of excess numbers.

Tropisms

Instinctive behavior plays an important role in the distribution of members of an insect population. The reaction of each individual to stimuli or to a pattern of stimuli causes the individual to remain in an environment compatible with its needs. If the individual is removed from such an environment, the reactions to the stimuli will enable it to return or find a new environment with the maximum compatible components.

The basis of instinctive behavior is in automatic responses to definite stimuli, and each such response is called a tropism. Each insect species exhibits a wide range of tropisms, a great number relating to sexual behavior and mating, and others relating to ecological factors of the environment. It is this latter group of tropisms that we shall consider here.

Phototropism, Reaction to Light. Most insects have an extremely well-developed response to light, moving toward the light source or away from it. Cockroaches move away from the light and are termed negatively phototropic; bees and wasps move toward it, and are thus positively phototropic. But the reaction often is different in various stages of an insect's life cycle. Housefly maggots are negatively phototropic and move away from light; adult houseflies are positively phototropic and move toward light.

Some aquatic insects, such as mayfly nymphs, maintain their dorsoventral position, that is, stay right side up, by orientation to light from above. This response is most pronounced when the insect is swimming, and is inhibited if the insect is at rest.

There is a definite response by some insects not merely to light in general but also to certain wavelengths of light. In most cases this is an aid to finding food or, in the case of ovipositing females, placing their eggs on the correct type of foliage. Thus, butterflies in search of food are guided by their perception of color in distinguishing yellow, red, and blue from green and approach the flowers of the former colors in preference to the green foliage. But some of these same butterflies will lay their eggs only on a green surface, which under natural conditions would be a healthy leaf suitable for larval food.

Geotropism, Reaction to Gravity. Many insects if placed in a vertical tube will go steadily to the top or bottom, rather than wandering haphazardly around the tube. Leafhoppers always go up; if the tube is inverted so that the insects are again at the bottom, they will start their upward climb again. This is a negative response to gravity, or negative geotropism. Other insects have a positive geotropism, normally going down or toward the earth. Many soil-inhabiting larvae such as wireworms have this reaction; thus, if they hatch from eggs laid on or near the soil surface, they burrow down into the soil.

Thigmotropism, Response to Contact. Many insects that normally live under bark, in soil, or in curled leaves have a well-developed touch or tactile reaction that causes them to remain in contact with some object, fig. 416. This is known as positive thigmotropism. Observation of the behavior involved indicates that the touch sensation acts as a sort of hypnosis, temporarily immobilizing the insect.

In all insects of active habits, the sense of touch serves as a detector of enemies. Frequently some area or structure at the apex of the abdomen, such as the cerci, has tactile hairs of extreme sensitivity to aid in these "escape" reactions.

Chemotropism, Response to Odors. The number of responses that insects make to various odors is legion. In relation to the environment these are mostly correlated with food, as in the case of an individual locating food for its immediate use, or of a female finding a suitable place for laying eggs in relation to the food of the resultant immature stages, fig. 417. In general, each insect is responsive to only the particular food odors that immediately concern the species. For instance, butterfly females of the genus *Macroglossa* will oviposit

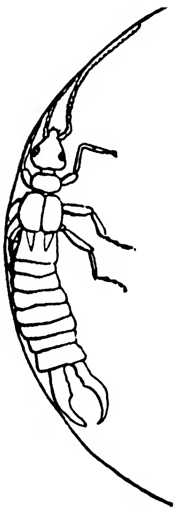

FIG. 416. An example of positive thigmotropism. Position taken by the earwig *Forficula* in a circular glass container. (From Wigglesworth, after Weyrauch)

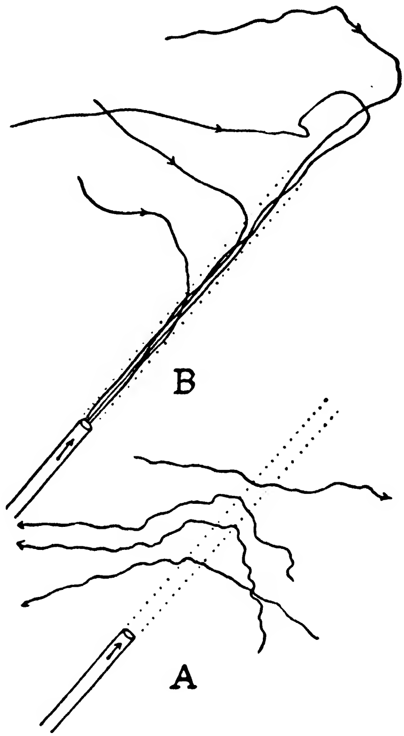

FIG. 417. An illustration of chemotropism. Tracks followed by *Drosophila* flies (deprived of wings) when exposed to (*A*) an odorless stream of air, and (*B*) air carrying odor of pears. (From Wigglesworth after Flügge)

only on a surface having the odor of the plant *Galium,* on which the larvae feed; other odors cause no oviposition response.

Most insects follow odor-laden air currents, orienting their line of approach either by direction of air current or by increase or decrease in odor intensity. There are some insects, however, that follow the trail of scent left by their prey as a dog follows a rabbit. The braconid wasp *Microbracon* follows the scent trail of its host, the larva of the mealworm *Ephestia,* the hunting wasp running along with its antennae held close to the ground. Ants use this method to follow trails to and from the nest, locating it by the routes marked with formic acid secreted and dropped by the ants.

Thermotropism and Hygrotropism. Insects respond to various degrees of heat and humidity, moving towards the condition closer to their optimum. Insects that feed on warm-blooded animals use temperature as a guide to their hosts. Thus, mosquitoes and bedbugs are positively thermotropic to temperatures near 98°F., that is, near mammal blood heat.

Coordinated Tropisms. Many activities of insects are dependent on responses involving two or more tropisms at the same time. It has been demonstrated, for instance, that ovipositing *Macroglossa* butterflies require both a green color and the odor of *Galium* to induce egg laying. Certain newly hatched caterpillars that feed in trees have both a negative geotropism and a positive phototropism, insuring that the larvae travel upwards to the natural food. In many other activities there is a fixed chain of responses, following each other in definite order. With the stable fly *Stomoxys,* different reactions to smell, taste, warmth, and moisture control the fly's approach to its animal host, the extension of its proboscis, probing of the host tissues, and, finally, feeding.

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10

Control Considerations

Losses due to insects have increased steadily in the United States with the expansion of farming and growth of population, as mentioned in Chapter 1. Natural enemies and periodic climatic reverses have failed to reduce populations of injurious insect species except for irregular intervals. It has therefore been necessary for man to devise and use various methods in an effort to reduce the populations of economic species or avoid losses caused by them.

HOW INSECTS CAUSE DAMAGE

Insects cause injury or damage to man and domestic animals, to a wide variety of crops, to stored products, and to buildings and many of their contents. Each item may be attacked by several or by many insect species, each causing a different type of damage. Sometimes the damage is direct, in that it is the result of the insect's own activities, such as feeding or oviposition. In other cases the principal damage is caused by a disease organism introduced into a plant or animal by the insect.

Direct Damage

Feeding–Chewing Type. Insects with chewing mouthparts, such as grasshoppers and caterpillars, as a rule cause the most conspicuous damage, because they remove a noticeable portion of the host.

Most readily noticed on plants is the work of forms feeding externally above the ground, since these attack leaves, fruits, buds, or twigs. Familiar examples are caterpillars on cabbage, fig. 419; grasshoppers feeding on corn, wheat, soy beans, and other crops; and adult

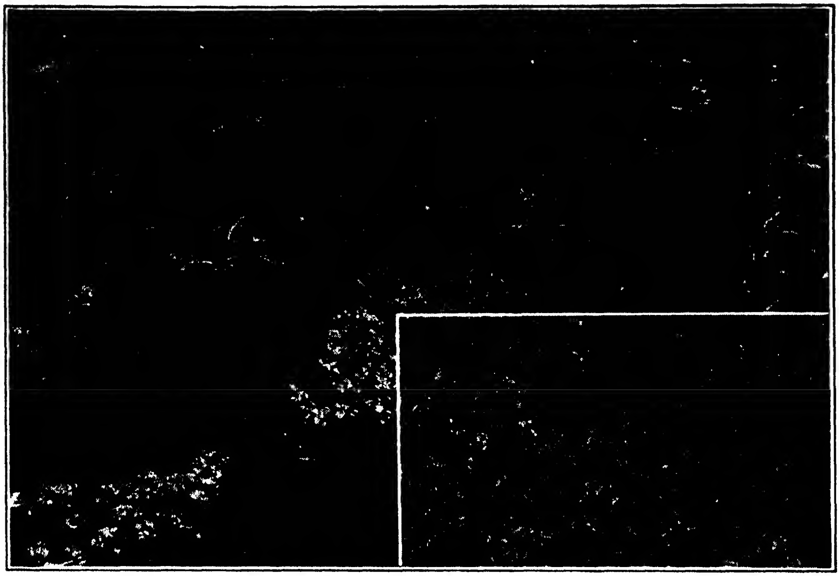

Fig. 418. Potatoes showing virtually complete destruction by the potato leaf-hopper; insert is a stand of healthy, sprayed potatoes taken on the same day to show contrast and condition. (From Illinois Natural History Survey)

Fig. 419. Two heads of cabbage from adjoining plats. *A*, sprayed for protection from insects; *B*, not sprayed and badly injured by chewing insects. (From Metcalf and Flint, after Wilson and Gentner)

Japanese beetles feeding on foliage and fruits of many trees. Another group includes a variety of small beetles, flies, and moths, whose larvae feed within the leaf tissues, and are called leaf miners. The spinach leaf miner *Pegomyia hyoscyanii* makes an irregular blotch in

Fig. 420. Mine of the spinach leaf miner. (After Frost)

the leaf, fig. 420; the aquilegia leaf miner, a minute fly, makes a winding serpentine mine, fig. 421.

Roots and underground tubers and bulbs are eaten by larvae of many beetles, flies, and a few moths. Root feeders may be inconspicuous, but, if they destroy sufficient root material, the plants either fall over or suffer from lack of moisture and nourishment. Excessive feeding by rootworms (larvae) of *Diabrotica* and related beetle genera causes serious lodging or stunting and death to corn stands, fig. 422.

White grubs, Japanese beetle larvae, and wireworms are other larvae that feed on roots. A variety of dipterous larvae, or maggots, attack roots; these include species feeding on onions, cabbage, corn, and soy beans. The maggots tend to feed on and in the larger roots and, when numerous, inflict serious damage or death to the plants. Larvae

FIG. 421. Mine of the aquilegia leaf miner. (After Frost)

of a few species of the fly family Syrphidae attack underground bulbs of tulips and other bulb crops, and a wide variety of beetle larvae attack tubers of Irish potatoes, and sweet potatoes, and root crops.

Boring insects are seldom seen, but there are many such species, and they cause considerable damage. Those attacking plants may bore into leaf petioles, branches, trunks, crown, fruits, or roots. Trunk and stem borers of living plants include larvae of clearwing moths (Aegeriidae), longhorn beetles (Cerambycidae), bark beetles (Scolytidae), and many miller moths. Twig borers and borers in herbaceous plants may remove so much tissue that the plant dies or is greatly weakened, becoming a prey to wind. Borers in trees may girdle the cambium layer, as do bark beetles, fig. 322, causing the death of the host. Others may tunnel through the heartwood and cause injury to the living host, and their tunnels may greatly reduce the value of the wood for lumber, fig. 423. All stages of powder post beetles (Lyctidae) and termites (Isoptera) bore into and eat

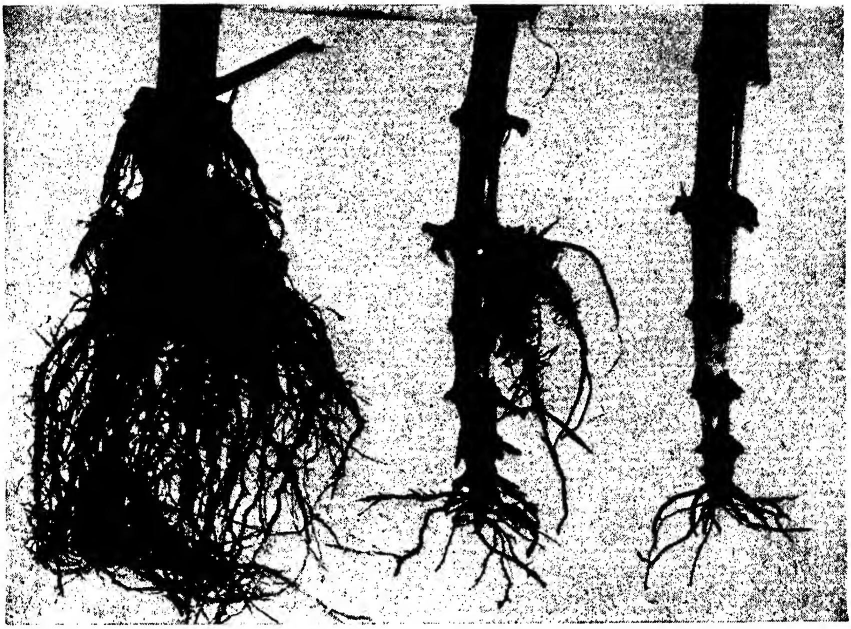

Fig. 422. Serious root damage to corn caused by rootworms of the genus *Diabrotica.* (After Tate and Bare)

deadwood. Borers in fruits include some of our worst agricultural pests such as codling moth larvae in apples; plum curculio larvae in plums, peaches, and cherries; and oriental fruit moth larvae in both twigs and fruits of peach and related fruits.

Man and other animals are also attacked by chewing insects. The entire order Mallophaga, the chewing lice, live externally on vertebrates, where they feed on skin, feathers, and surface debris. Several fly families have species whose maggots live in dead animal carcasses and a few which attack living animals. The screw-worm fly larva *Cochliomyia americana* gains entrance into the body of mammals by way of a wound and continues to eat through live tissue under the skin. Maggots of the fly families, Oestridae and Gasterophilidae, live internally in the bodies of animals—in the stomach, nasal passages, or under the skin. There is some question as to how these maggots feed, but at least in the full-grown stages they simply suck in gastric

FIG. 423. Injury by the locust borer. (From the Connecticut Agricultural Experiment Station)

contents or secretions produced by the host animal, without any cutting or chewing by the larval mouthparts.

Feeding-Sucking Type. Insects having piercing-sucking type of mouthparts leave no gaping wounds but sap the vitality of the host. As these insects feed, they pump saliva into the feeding puncture or wound, and frequently the physiological reaction of the host to this saliva is worse than the effect of the withdrawal of blood or sap. For instance, horses may be killed by the bites of blackflies, death resulting from a pathologic reaction to the blackfly saliva rather than from loss of blood.

Fig. 424. Hollyhock leaves showing effect of feeding by plant bugs. At left, little feeding; at right, excessive feeding that has caused complete etiolation. (From Illinois Natural History Survey)

Fig. 425. Leaf curl on snowball caused by aphids. Normal foliage at left, infested foliage at right. (From Illinois Natural History Survey)

On living plant leaves sucking insects empty the plant cells, removing the green color and causing a whitening or etiolation followed by production of scar tissue. Each feeding puncture results in a tiny white spot, and, when they are extremely numerous, the entire leaf may appear blanched, fig. 424. Frequently curling of the leaf follows heavy feeding, as in fig. 425. On fruits the feeding punctures cause the formation of scar tissue called catfacing, fig. 426. Sucking insects attacking roots or stems rarely produce feeding symptoms other than the reduced vitality or wilting of the host.

Vertebrates suffer from many more species of sucking insects than from chewing insects. Sucking lice, mosquitoes, horseflies, and fleas are examples of large groups that attack vertebrates almost ex-

Fig. 426. Catfacing of peaches caused by feeding of plant bugs. (From Illinois Natural History Survey)

clusively. Feeding punctures, or "bites," of these insects usually cause a local irritation accompanied by swelling. Individuals react differently, however, so that no general diagnosis of the effect of bites can be given. The actual damage inflicted by these insects is twofold: (1) irritation, loss of blood, pathologic reaction, and loss of condition of the victim, and (2) the possible transmission of certain diseases by some of the insect species. This latter is discussed in a later section of this chapter.

Injury by Oviposition. A few groups of insects damage plants by laying eggs in them, fig. 427. Tree crickets of the genus *Oecanthus* drill rows of egg cavities in raspberry and blackberry canes and in twigs of fruit trees, causing a later splitting or decay of the injured stems. Cicadas (Cicadidae) and treehoppers (Membracidae) cause the same type of injury to many kinds of fruit and shade trees. The feeding of these insects causes little damage, or it may occur entirely

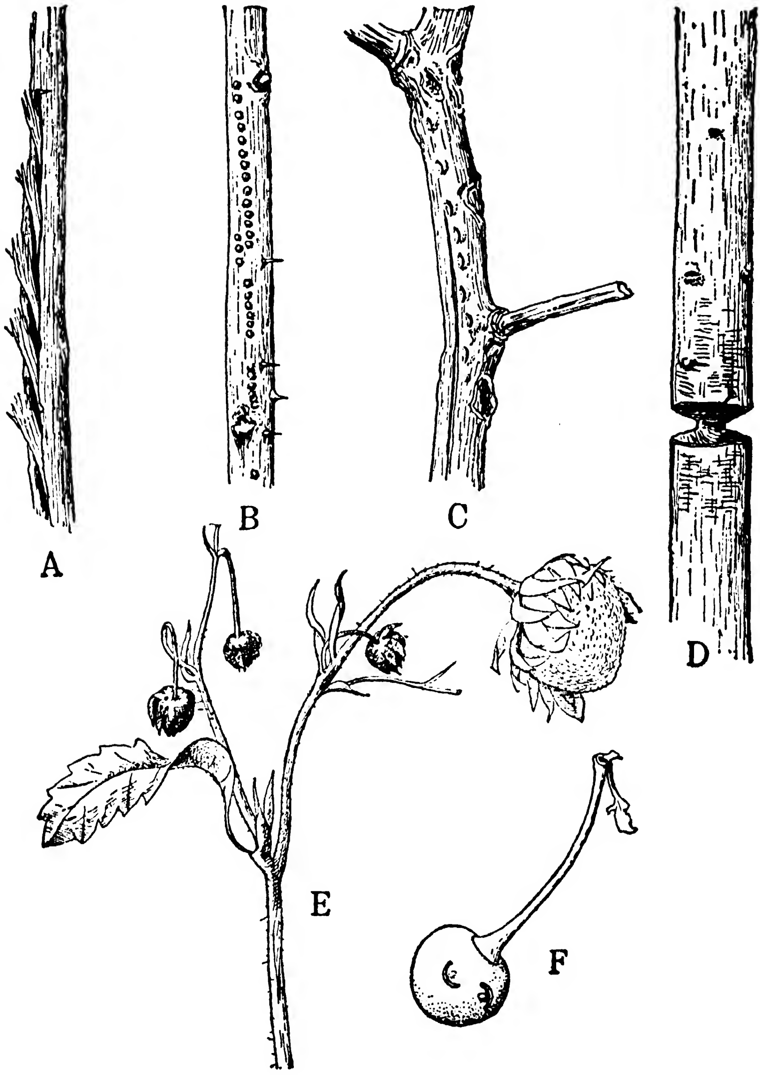

Fig. 427. Examples of injury to plants caused by egg laying. *A,* twig split by egg laying of the periodical cicada; *B,* holes in stem of raspberry made by egg laying of a tree cricket; *C,* slits in bark of apple twig beneath which a treehopper has thrust her eggs; *D,* twig of pecan cut nearly in two by egg laying of female twig girdler; *E,* fruit buds of a strawberry, partially severed by strawberry weevil after laying egg in the buds; *F,* cherry showing two egg punctures of the plum curculio. (After Metcalf and Flint, "Destructive and Useful Insects," by permission of McGraw-Hill Book Co.)

on non-economic herbaceous plants in which the insects do not oviposit. Fruits may be injured and buds stunted by egg punctures.

Spoilage. The damage some insects cause is due to spoiling a product rather than feeding on it. The hop aphid *Phorodon humuli* usually causes little injury to the development of the hops; aphids feeding in the hop cones, however, produce honeydew (feces) which provides a growth medium for molds. This discolors the hops and greatly reduces their market value. Cockroaches in houses and stores drop feces on various merchandise, causing discoloration and sometimes an offensive odor, which reduce the value of the merchandise. On greenhouse and truck crops, insect webbing, aphid honeydew, or frass will often result in drastic reductions in sale value of the crop.

Stings and Other Irritants. There are some protective devices of insects that cause injury or extreme irritation, such as bee and wasp stings, ant bites, and nettling or poison hairs of certain caterpillars. Although very unpleasant and painful, these are only a negligible part of insect injury as a whole.

Transmission of Plant Diseases

Insects affect certain plants seriously by disseminating plant diseases. In many instances the diseases are much more destructive than the insect injury by feeding. Under these circumstances control of the disease may resolve itself into a problem of very thorough control of the insect, because even a few insects would be able to inflict, indirectly, staggering losses.

A number of plant diseases, not actually carried by insects, gain entrance to the plant through insect feeding or oviposition punctures. Brown rot of peach commonly enters through feeding punctures of plum curculio adults, and bacterial rot of cotton through feeding and oviposition punctures of various insects.

Insects assist in the dissemination of some plant diseases by transporting them on the body or in the digestive tract. Fire blight is carried on the legs and body of bees, beetles, and some other insects, as well as by birds and other animals. Spores of certain fungus diseases, such as apple canker, are eaten by insects and pass through the digestive tract in healthy condition. In these cases insects are only one of many ways by which the disease is spread.

More important are cases in which insects are the principal or sole transmitters or vectors of a disease from one plant to another. The insects become infected with the disease, usually either bacterial or virus, by feeding on an infected plant; some of the disease organisms are injected either mechanically or with the saliva into the tissues of the next plant on which the insects feed. Various species of leafhopper transmit aster yellows, and the beet leafhopper transmits curly top of sugar beets, both virus diseases. Many other virus diseases are transmitted by other insects. Bacterial diseases such as cucurbit wilt disease are carried by insects. In cucurbit wilt the bacteria pass the winter in the digestive tract of the hibernating vectors, the cucumber beetles, which start the next year's infections. Many of these virus and bacterial diseases are exceedingly destructive.

Transmission of Animal Diseases

Some of the most important diseases of man and other vertebrates are transmitted by insects. As with plant diseases, in some cases insect transmission is only one of the several ways by which the disease is spread, and in other cases the insect vector is the only known agent by which the disease is disseminated from one host individual to another.

In the first category are typhoid fever, summer diarrhea, and some kinds of dysentery, all caused by species of the bacterial genus *Bacillus*. Houseflies get the disease organisms on feet or mouthparts through contact with sewage, saliva, or other infected material and then contaminate food or other items on which they alight later. These diseases are transmitted in a variety of mechanical ways, but under some particular conditions flies may be the principal effective method of dispersal of the diseases.

Bubonic plague (the black death), caused by *Bacillus pestis*, is another contagious disease belonging in this first category. Rats and small mammals serve as the reservoir of the disease, and rat fleas carry it from rat to rat or from rat to human.

Insects are the sole vectors of several important human diseases. Malaria is caused by species of the protozoan genus *Plasmodium*, transmitted from one person to another by some species of mosquitoes belonging to the genus *Anopheles;* yellow fever and dengue (breakbone fever), caused by virus organisms, are carried by several species of mosquitoes of which *Aedes aegypti* is the chief vector in North America; African sleeping sickness is caused by protozoans of the genus *Trypanosoma*, which are carried by flies of the genus *Glossina;* elephantiasis (filariasis), caused by nematode worms of the genus

Filaria, is transmitted by several species of mosquitoes. In all these instances the mosquito or fly, when feeding on a diseased person, draws up into its buccal cavity or digestive system some of the disease organisms; some of these are discharged during feeding at a later date into the tissues of another person. In this manner healthy persons are inoculated with the disease.

Typhus is caused by an almost ultramicroscopic organism called *Rickettsia,* which is carried by body lice or cooties. These take up disease organisms when feeding and then later expel them in the feces. Scratching on the part of the bitten person works the disease organism into the skin and effects inoculation.

Ticks and mites are the only known vectors of several important diseases, of which three are of especial interest. Texas fever, lethal disease of cattle, is caused by a species of Sporozoa, *Babesia bigeminum.* The disease organisms are transmitted by the cattle tick *Margaropus annulatus.* Rocky Mountain spotted fever is a highly fatal human disease of increasing incidence, caused by a *Rickettsia* organism. This disease is maintained in some of the small wild rodents, and a few species of ticks of the genus *Dermacentor* effect the transfer of the disease by feeding on infected rodents during nymphal development and afterwards, when adult, biting man. A third disease is scrub typhus, an oriental disease caused by another *Rickettsia* organism. This is transmitted from wild rodents to man by chiggers (early instars of the mite family Trombidiidae) and was a serious hazard to humans in both the Burma and Pacific theaters during the battle of Japan in World War II.

Under most circumstances the practical control of these diseases is obtained by control of the vectors. This has been particularly effective in the case of Texas fever; control of the cattle tick has virtually eliminated the disease from the United States. Extremely satisfactory results have been obtained also in reducing outbreaks of typhus by controlling body lice. Mosquitoes, flies, and *Dermacentor* ticks are more difficult to control, and the species involved have a wide dispersal range so that measures aimed at control of these vectors have not always produced such remarkable results as those obtained with Texas fever and typhus.

A SURVEY OF PEST INSECTS

In North America some ten thousand different species of insects are of economic importance in varying degrees. Of these about one thousand species are the persistent pests that cause the greater proportion of our insect damage. It is not proposed to give here a detailed discussion of these, but instead to present a brief survey of the most destructive species in relation to the crops or commodities they attack, or the damage they do.

Agricultural Crop Pests

By far the greatest number of important insect pests attack farm crops and animals. Injury is of many types, and insect species of widely different habits are involved.

Field-Crop Insects. All the major field crops with the possible exception of soy beans suffer high losses from insect attack. Serious enemies of cotton are the boll weevil, which feeds inside the boll, destroying the developing cotton fiber; the cotton leafworm, whose larvae eat the foliage; and the cotton aphid, which sucks juices from the leaves and stems. Corn may be almost completely destroyed by grasshoppers feeding on the foliage or by chinch bugs sucking the plant juices. The corn yield is annually reduced by several species of borers in cobs and stalks, including both the European corn borer and the western corn borer. Wheat and other small grains are injured extensively by various species of cutworms, wireworms, aphids, and grasshoppers, depending on climatic conditions and region. Larvae of the hessian fly attack the stems and crowns of grains; and this species is the most destructive single pest attacking wheat. Field enemies of tobacco, a high cash-value crop, are chiefly leaf feeders, such as hornworms and flea beetle adults; cutworms and tobacco budworms also cause serious damage. The potato beetle feeds on potato foliage, and various leafhoppers suck the plant juices. Potato tubers are injured by soil-inhabiting larvae such as wireworms and flea beetle larvae.

Other field crops are attacked by insects of general feeding habits, such as grasshoppers. Each crop has in addition certain pests more specific in their host preference. The most notable exception is the soy bean crop; although attacked sporadically by a variety of general feeders such as grasshoppers and root maggots, it does not appear as yet to have insect enemies of serious importance.

Truck Crop and Garden Insects. Each plant species grown in truck farm or garden is subject to ravages from one or more insects specific in their food preference. These include such insects as cabbage loopers, cabbage butterflies, and cabbage aphids, that feed on cabbage, cauliflower, and other cruciferous crops; the carrot rust fly, specific on carrots; melonworms, asparagus beetles, and the Mexican bean beetle. In addition to pests specific to each crop, there are many general feeding insects that may attack almost any of these crops. Garden webworms, grasshoppers, blister beetle adults, cutworms, and fall armyworms are among the group most likely to occur occasionally in destructive numbers.

Fig. 428. Injury caused by the chrysanthemum midge *Diarthronomyia hypogaea*. About natural size. (From Metcalf and Flint, "Destructive and Useful Insects," by permission of McGraw-Hill Book Co.)

Greenhouse Insects. In the greenhouse, warm humid conditions are maintained throughout the winter months. As a result we find in them many insect species that are normally tropical and subtropical in distribution. Most troublesome of these are several species of thrips, mealybugs, and scale insects. In addition, several species that are outdoor in habit during the summer invade greenhouses and continue active all winter, instead of becoming dormant. The melon aphid, green peach aphid, and the greenhouse leaf tier are examples of this type.

The different kinds of plants grown under glass are legion, and few are not attacked either by general feeding insects like larvae of leaf tiers or by specific pests such as the chrysanthemum midge, whose larvae make galls on leaves and stems, fig. 428. Normally forty to fifty species of potentially destructive insect species are found during the winter season in greenhouses. When one considers the variety of hosts involved and the fact that these may all occur in a range of glass of only a few thousand square feet, it poses a serious control problem and demands constant alertness on the part of the operator.

Fruit Insects. All classes of fruit—citrus, deciduous, and small—suffer heavily from insect damage, and in each group the major pests are different.

Citrus-fruit trees are injured mostly by scale insects, mealybugs, whiteflies, thrips, and mites. The purple scale, California red scale, and black scale are especially important, damaging fruit and trees or producing honeydew on which grows a black sooty fungus that discolors the fruit. Many of the scales on citrus have a wide host range, but, being subtropical in distribution, they are pests of other fruits only in the citrus belt, in Florida, southern Texas, and southern California.

Deciduous fruits, including apple, pear, cherry, peach, plum, and their allies, have many destructive pests. Apple fruit is attacked chiefly by larvae of the codling moth. This insect is the most important species on the apple control calendar. Peaches, cherries, and other soft fruits are entered by larvae of the plum curculio, which also attacks apples. The branches and foliage of the entire group suffer from San Jose scale, oriental fruit moth, aphids, red spiders, a host of leaf-feeding species, and many that bore in the tree or deform the fruit.

Small fruits are a group of wide taxonomic composition and have more specific insect pests. Grapes are attacked by the grape berry moth, many aphids and leafhoppers, and leaf-eating beetles that eat roots and leaves. Currants, raspberries, and strawberries are attacked by a variety of aphids, leaf-feeding larvae, and stem or crown borers.

Insects of Man and Domestic Animals

Both man and domestic animals suffer annoyance and exposure to disease from the activities of insects. Certain of these insects, such as the Anoplura, confine their attacks to one or two closely related species of animals. Others, such as mosquitoes, are general feeders on a wide variety of warm-blooded vertebrates.

Domestic fowl are attacked chiefly by Mallophaga (chewing lice) and mites, several of which live on hens, ducks, turkeys, and geese. On young fowl infestations of lice often cause death; on older birds the lice cause lack of condition and lower egg production. Mites sometimes become very injurious by reducing the general health of the flock. Blackflies transmit at least one duck disease similar in many respects to malaria. Hens suffer also from attacks of specific fleas, of which the southern sticktight flea is the most persistent.

Domestic animals and man have a variety of specific parasites, including Anoplura (sucking lice), fleas, bedbugs, a few Mallophaga, and several kinds of mites. These latter include such annoying forms as itch mites, chiggers, and ticks. Sheep have in addition "sheep-ticks"; these are odd wingless flies of the family Hippoboscidae. Attacks by ectoparasites result in irritation and loss of condition, but seldom in death unless disease transmission is involved.

Several vertebrates are attacked internally by larvae of bot flies and warble flies. In the horse the larvae attach to various regions of the digestive tract and cause severe loss of weight and condition. Warble flies develop in the sinuses of sheep and, in the later stages, along the back of cattle where they form a pocket just beneath the hide. Larvae of the screw-worm fly enter wounds, feed beneath the skin, and annually cause large losses to all kinds of livestock.

In addition to these and other specific pests, all warm-blooded vertebrates are attacked by a great number of bloodsucking flies—mosquitoes, horseflies, blackflies, *Symphoromyia* flies, stable flies, and horn flies. Some of the fleas, ticks, mites, and bedbugs are also general feeders. The annoyance these cause is often severe. Blackflies especially may be destructive and occasionally cause the death of large numbers of horses and mules in local areas. Mosquitoes, blackflies, and horseflies are at times abundant enough to cause an exodus of tourists from an area, to reduce land values near suburban centers, or to retard settling of large tracts, as in the extreme northern part of Canada and in Alaska. The effect of these attacks on livestock in general may result in a loss of condition equal to or greater than that caused by specific parasites.

The greatest potential injury to man and animals by insects is through insect-borne diseases. As previously mentioned, insects transmit some of the most destructive diseases of vertebrates. During war the danger from insect-borne diseases is greatly increased, because men are concentrated together under conditions in which sanitation and insect control may be difficult, and the crowding offers good opportunities for the rapid spread of disease.

Stored-Food-Products Pests

Grain and meat, flour, grain meals, and other highly nutritious foodstuffs are eaten by many insects. When in storage, these commodities suffer a heavy loss from insect ravages and necessitate constant preventive and remedial measures to keep them to a minimum.

In North America the chief pests of stored grains and grain products are the adults and larvae of the sawtooth grain beetle, the confused flour beetle, cadelle, mealworms, and the granary and rice weevils; and the larvae of the Indian meal moth and the Mediterranean flour moth. Peas and beans in storage are eaten by various pea weevils (Bruchidae). Meats and cheeses are eaten by larder beetles and maggots of the cheese skipper.

Large quantities of stored foods are attacked first by the group of insects just listed. After a certain amount of damage is done molds enter, followed rapidly by a host of other insect species, and soon the entire mass of food may be reduced to a small percentage of the original.

Pests of Human Habitations

Some insect species have become almost "domesticated," especially north of the frost line, in that they are found almost entirely in human habitations. In the case of ectoparasitic species the relationship antedates civilization and is due to the parasites staying with the warm-blooded host. With other species, however, the relationship is more recent and is due to the relatively high temperatures at which houses and buildings are maintained even through severe winters. Thus some species, originally semitropical, are now found much farther north and are able to maintain themselves in human habitations.

Ectoparasites and pests of stored foods are of prime importance in human habitations. In addition, larvae of clothes moths and carpet beetles eat anything containing animal fibers, such as woolen garments, upholstery, and carpets. Silverfish and cockroaches are general feeders that eat starchy foods such as bookbindings and are an unsightly nuisance. Cockroaches drop excrement promiscuously and spot and taint food and quarters; when very abundant, they will give a house, store, or restaurant a disagreeable and penetrating odor. Ants frequently invade buildings and may become a serious nuisance in the kitchen and food-storage rooms.

Termites are the most destructive pests of buildings. They eat the wood in foundations, flooring, and walls, necessitating extensive repairs. Other insects live in wood in dwellings, such as Lyctidae beetles, and carpenter ants may eat out extensive galleries in wood of buildings to use for nests. But of all insects that attack the actual building, termites are by far the most formidable.

Shade Tree and Forest Insects

Trees in general support thousands of insect species, which may defoliate, girdle, or bore into the tree, or suck its juices. Many of these species have only a slight effect on the host tree, but some damage the tree severely or may even kill it. As a result there is a high annual loss in both shade and forest trees.

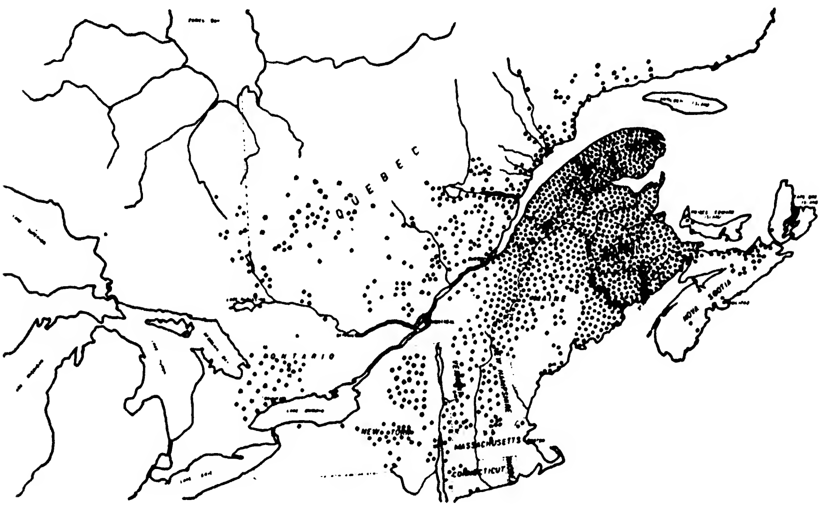

Fig. 429. Distribution of the European spruce sawfly in North America during the epidemic of 1938. (Modified after Balch)

Shade trees in the northeastern states are attacked especially by the gypsy and brown-tail moths. Elms suffer most from the elm leaf beetle and from Dutch elm disease, carried from tree to tree by the small European elm bark beetle. Direct injury by bark beetles and wood borers weakens and kills trees of many species.

Forest trees are visited periodically with insect outbreaks that kill huge tracts of timber. This is a loss of natural resources that in past years was given little attention, but, now that our forests are dwindling, increased efforts are being made to find means of checking losses. Larvae of forest tent caterpillars, gypsy and brown-tail moths, hemlock loopers, budworms, and tip moths are perennial defoliators of various deciduous and evergreen trees. Bark beetles are the greatest single enemy of conifers, especially in the West. Sawflies feeding on conifers occasionally appear in outbreak numbers and may cause tremendous damage. The most recent large sawfly outbreak was of the introduced European spruce sawfly, which in 1938 defoliated about twelve thousand square miles of spruce timber, chiefly in the eastern provinces of Canada, fig. 429.

NATURAL CONTROL

From time to time insect pests of many kinds are reduced to insignificant numbers by inimical factors of the environment, such as drought, parasites, or disease, as discussed in Chapter 8. The European spruce sawfly, for instance, has been virtually exterminated in large areas by a bacterial disease. In 1935 the chinch bug was reduced to the status of a rarity in many corn-belt states by adverse winter conditions plus a fungus disease. But these phases of natural control are unpredictable and non-operative for long periods of time. Furthermore some of our worst pests, such as the codling moth, apparently have at most only partial or insignificant natural checks and so are a menace every year.

In order to protect his interests, it has therefore been necessary for man to devise means of combating insects by his own efforts. This type of control is called *artificial control,* in contrast to the natural control effected by the unaided environment.

CONTROL METHODS

In artificial control a great many different methods have been found to reduce the numbers of individual pests. These methods fall into a few general categories and are treated briefly in the following paragraphs.

Quarantine

The most obvious way to avoid damage by an insect is to prevent its becoming established in a country if it is not already there. There are hundreds of insects in other parts of the world, especially in temperate areas of Europe and Asia, which we believe might become pests of great economic importance if established in North America. To prevent their entrance, the United States Federal Government maintains an inspection of imports into the country, especially living plants or animals or packing material that is likely to harbor pests and serve as a carrier for them. Most or all of this material is fumigated before being allowed into the country. In addition, states may

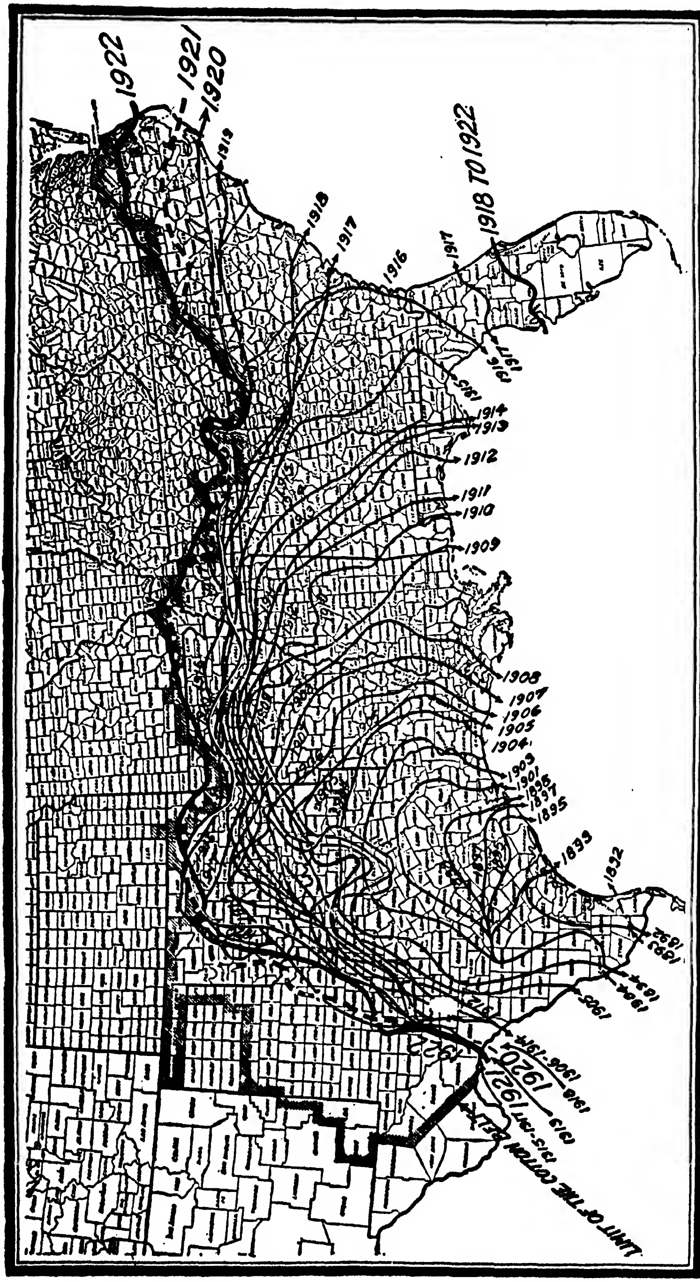

FIG. 430. The spread of the cotton boll weevil in the United States, up to 1922. (From U.S.D.A., B.E.P.Q.)

have restrictive regulations regarding the movement of critical materials within the state or into the state. The Canadian Government maintains a similar service.

It is admittedly impossible to prevent indefinitely the entrance of all potential new pests into the country, but quarantine records show that hundreds and sometimes thousands of new importations are prevented every year. It is impossible also to estimate how much we gain by this. Experience with such destructive importations as the cotton boll weevil, fig. 430, the European corn borer, and the Japanese beetle, however, emphasizes that we cannot afford to take the chance of allowing free entry to every insect species.

Biological Control

The possibility of propagating and distributing natural enemies for the control of destructive insects has kindled the imagination of the entomologist for many decades. It has been found, however, that with destructive insects endemic to the United States we can do little to improve on existing natural control. Representing the evolutionary product of great geologic time, natural control has usually reached a peak that cannot be raised profitably by artificial means.

With introduced pests the situation is entirely different. The particular species may have an abundance of parasites or predators holding its numbers in check in its native land. When it is accidentally introduced into another country, usually only the pest without its parasites is transported. Freed from enemies, the pest in the new land is able to flourish at an unimpeded rate.

The ideal control for such an introduced pest would be to establish efficient enemies of it so that they would reduce the numbers of the pest to insignificant proportions. This might result in a permanent control that would obviate the necessity for an annual program of more expensive measures.

This ideal has been achieved only rarely. The most outstanding example has been the control of introduced cottony-cushion scale by the importation and establishment of the Australian vedalia ladybird beetle. So effective are the beetle and its larvae in controlling the scale in California that only occasionally and locally does the scale become important as a pest. Many parasites, especially of introduced pests such as the Japanese beetle, gypsy moth, and European corn borer, are imported by the U. S. Bureau of Entomology and Plant Quarantine, and released in the United States. Many imported parasites fail to maintain themselves in the United States under natural conditions, owing undoubtedly to their lack of adjustment to climate or the lack of availability of suitable hosts at the right time. Some species have become successfully established and aid in controlling the pest species. It is hoped that eventually sufficient parasite populations will be built up so that the populations of many pest species will drop well below their present destructive level. In some areas this result has already been achieved for the satin moth by introduced hymenopterous parasites, especially in Washington State and British Columbia. Propagation and dispersal of bacterial diseases of Japanese beetles have also given promise of being effective.

Sufficient work has been done in biological control to show that a number of factors influence its success or failure. A few of these factors are the ecological requirements of the parasites, their effect on each other, their host specificity, their rate of increase, and the character of their dispersal. To be tried effectively, well-trained personnel and a great amount of specialized equipment are necessary, together with an organization for gathering parasite material in foreign countries and getting it into the United States alive and healthy.

Because of these conditions, the work on biological control in the United States is done chiefly by the Federal Government. The final distribution and liberation of parasites are often performed cooperatively by scientists of the Federal Government and interested state agencies. The British Government is also extremely active in biological-control efforts. The Imperial Parasite Laboratory, moved during the recent war from England to Belleville, Ontario, is the central point of an organization for collecting, rearing, and shipping parasites of destructive insects to all parts of the British Empire.

Cultural and Management Control

Some insect pests of agricultural or forest crops may be kept below the damage level by various cultural or management practices.

An important general approach is keeping crops healthy, by proper fertilizing, drainage, irrigation, and cultivation, and by planting crops that are well adjusted physiologically to the climate and soil.

Against certain pests specific cultural methods are of value, such as clean cultivation, crop rotation, certain times of harvesting or planting, and the use of insect-resistant or tolerant varieties.

Clean cultivation eliminates weeds that may serve as host to insects that attack the crop. The buffalo treehopper breeds on many herbaceous weeds; the adult hoppers fly into adjacent fruit trees, cut slits in the twigs, and in them lay their eggs. Clean cultivation of an orchard prevents this injury by eliminating the primary host. Weeds and soil debris also serve as hibernating or pupating quarters for a wide variety of harmful insects, and clean cultivation tends to discourage a build-up of population in that area.

Crop rotation has been found especially effective against some insects whose larvae live in soil and feed on roots. *Diabrotica* rootworms can be controlled by crop rotation. These beetle larvae feed primarily on corn roots. If corn is grown continuously on the same ground for over three years in localities favoring these insects, they build up large populations and cause severe damage to corn. If, however, corn is eliminated and wheat or legumes substituted for a year, the rootworms starve. For this reason a rotation of corn with wheat or other crops arranged so that corn follows corn for no more than 2 or 3 years eliminates rootworm damage almost completely.

Choice of time of planting crops is useful as a control measure for certain insects. The hessian fly, a serious wheat pest whose larva feed in the leaf sheath of wheat, can be successfully controlled by regulating the time of planting winter wheat. The entire fall generation of adult midges normally emerges within a short period, following late summer rains. The adults live only 3 or 4 days, laying their eggs in grooves of wheat leaves. If winter wheat is planted after this generation is past, the plants will have no eggs laid on them and consequently will be entirely free from attack until spring. To take advantage of these conditions entomologists in wheat-growing areas have established dates for sowing winter wheat that will (1) allow the plants enough good weather to attain satisfactory growth before winter, and yet (2) be late enough to avoid all but a light infestation of hessian flies, fig. 431. The spring generation of hessian flies attacks only late shoots (tillers) of winter wheat and does little damage.

Early or late planting of corn and other crops is sometimes of assistance in reducing infestation and damage by such pests as rootworms and European corn borers.

In forestry, time of cutting a timber crop has proved of value in preventing outbreaks of some extremely harmful insects. It has been found that some of the most destructive species of bark beetles build up outbreak populations in over-age stands of pine. By cutting the trees for timber before they reach old age, this beetle population increase is prevented, and younger trees in the stand are given a better chance of development.

Another important phase of cultural control is the selection of species or varieties of plants that are resistant to or tolerant of insect attack. This is as yet the most successful general method for preventing damage by the European corn borer. It has been found that certain varieties of corn have an unusually strong stalk that will withstand heavy infestations of corn borer larvae without becoming critically weakened. Less tolerant varieties having the same borer infesta-

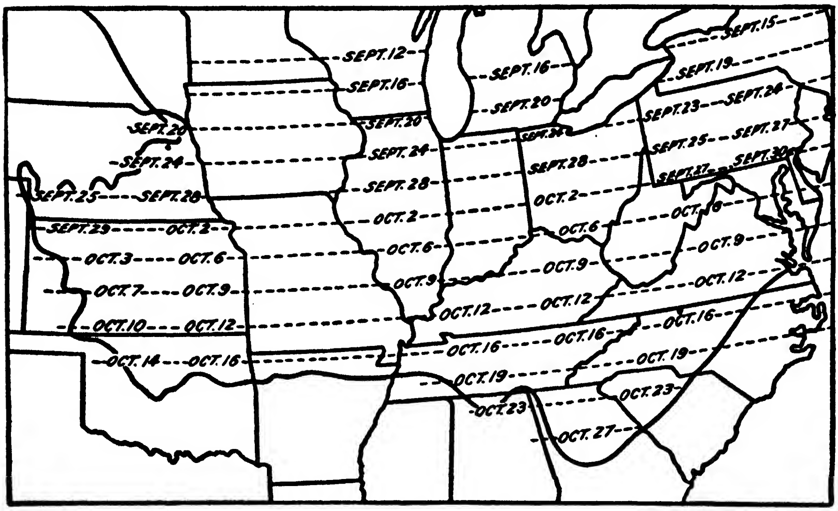

FIG. 431. Average safe dates for sowing wheat in several north central and eastern states to escape injury by the hessian fly. (From U.S.D.A., B.E.P.Q.)

tion break off and lodge, resulting in lower yield and greater difficultiès in harvesting the crop.

This same crop-selection principle is used as a remedy for the gypsy moth. We have already mentioned that, for its successful early development, one of the species' favored hosts is necessary, but that later instars move over to pines and other non-favored species, which they may defoliate. To decrease infestation by this pest, the favored host species are kept to a minimum and replanting is done with other species.

Mechanical Control

If it is necessary to use more direct methods than those previously mentioned in order to obtain control of an insect, there are several that can be followed. The simplest is mechanical control, which includes removing insects by hand or using mechanical devices to trap or kill them.

Hand picking is practiced on large caterpillars such as tobacco or tomato hornworms. The number of insect individuals is usually only moderate, and the individuals are large in size and easy to see. Nests of larvae can be cut out of trees and destroyed. A number of mechanical devices are used with good effect against a limited number of pests. One of the most common is screening, both screen doors and window screens, to keep insects out of buildings. Various traps of the maze type are used to catch flies. Bands of burlap or paper are fastened around trunks of fruit trees to provide hibernating or pupating quarters for codling moths; periodically these bands are examined and the insect occupants killed. Bands of screen, gauze, or sticky substances are put around trees to prevent ascent of wingless female moths and larvae, fig. 432.

FIG. 432. Banding traps used to prevent ascent of larvae and wingless female moths. (From U.S.D.A., B.E.P.Q.)

Against migrating wingless insects, such as Mormon crickets or chinch bugs, attacking field crops, various mechanical barriers are used, especially furrows in the soil or wooden or paper barriers. An insecticide is often incorporated into the barrier to insure its effectiveness.

Physical Control

We have noted previously that insects can endure only limited extremes of heat, cold, and other physical phenomena. This limited endurance is utilized to kill insect pests. It is difficult to control such physical factors over a large space, so that with a few exceptions their use is restricted to buildings and tight enclosures.

Superheating is employed by many mills and elevators as a control measure. During hot weather in summer, the building heating plant is used to raise the temperature to about 140°F. for several hours, and this kills all the insects in the building.

Cooling is used extensively in storage for insect control. Furs, tapestries, and other valuable articles of animal origin are kept in lockers below 40°F. This does not kill the insects, but at this temperature they are completely inactive and do no damage.

Electricity is used to some extent to kill insects. Screens and lights can be fitted with electrically charged grills that electrocute insects coming between the elements.

Chemical Control

Various chemical compounds are toxic or repellent to insects and are used extensively for their control. Because it is usually more expensive, such chemical control is applied when control by other methods is too slow or too ineffective.

Types of Chemicals. Toxic compounds may be divided into four categories: stomach poisons, contact poisons, fumigants, and repellents.

Stomach poisons are substances that kill the insect when they are eaten and taken into the digestive tract. The most widely used are the arsenicals, especially Paris green, lead arsenate, and calcium arsenate. Hellebore and fluorine compounds such as sodium fluoride and sodium fluosilicate are also commonly used stomach poisons.

Stomach poisons are used primarily against insects that have chewing mouthparts and bite off and swallow portions of the food. The poison is applied to the surface of the food as a spray, dip, or dust, and the insect is sure to take some of it with its meal. Against some insects such as ants and grasshoppers, the poison is mixed with an attractive bait put where the insect can find and eat it. For ants the baits are usually liquid and are set near nests or runways. For grasshoppers the baits are usually of bran or some carrier similar in texture and are spread broadcast in the fields.

A remarkable type of stomach poison has been demonstrated by several investigators. Apparently some plants are able to absorb and translocate certain poisonous compounds in sufficient quantity to kill insects feeding on the plant. Potatoes sprayed with Bordeaux mixture (a copper compound), and bean plants sprayed with derris show this phenomenon. Ornamental plants grown on soil containing selenium absorb the latter, which kills mites and insects feeding on the plants; this method cannot be used on edible crops, however, because of the extreme toxicity of selenium to humans and livestock. The affected insects observed to date include mostly aphids and leafhoppers, which have sucking mouthparts and feed on internal contents of cells, or on plant sap.

Contact poisons kill the insects by contact without being swallowed. Often the lethal agent is a gas that enters the spiracles and

FIG. 433. Application of insecticides; the use of airplane equipment has been of great aid in many situations. (From Ohio Agricultural Experiment Station)

causes suffocation, as in the case of nicotine; in other instances the lethal compound may affect the nervous system.

Until about 1940, the principal contact poisons in use against insects were nicotine alkaloid (volatile), extracted from tobacco; pyrethrum, extracted from the dried flower heads of certain species of the aster genus *Chrysanthemum;* sulphur and several sulphur compounds; and several lubricating oils, miscible oils, and oil emulsions. Since 1940, there have developed a number of synthetic organic compounds, such as DDT [1-trichloro-2,2-bis(p-chlorophenyl)ethane], chlorodane, and tetraethyl pyrophosphate, that are far more toxic to many insects than the contact poisons of older vintage.

Contact poisons are of especial use against insects having sucking mouthparts, such as aphids, which do not take up poisons applied to the food surface; insects that cannot be reached when feeding, such as bottom-feeding mosquito larvae which are killed by contact poisons when they come to the surface for oxygen; and insects such as adult mosquitoes that are scattered generally throughout an area. Contact poisons toxic to a variety of insects have the advantage of killing both the sucking and chewing insects at the same time. These poisons are applied as a dip, dust, spray, or colloidal mist (aerosol).

Fumigants are toxic gases, usually applied in an inclosure such as a box, building, or tent. Compounds in general use are hydrocyanic acid, nicotine, paradichlorbenzene (PDB), methyl bromide, and chloropicrin. The use of fumigants is aimed at killing all the insects in the inclosure, and fumigants are employed commonly to rid houses, greenhouses, warehouses, stores, mills, and elevators of insects. Box fumigation is used for small quantities of material, such as clothing. In the recent World War fumigation stations were used extensively to rid clothing of lice and other vermin.

In California gastight tents are used to inclose citrus trees for fumigation with hydrocyanic acid, fig. 434. Prior to fumigation buildings need to be checked for gas leaks and the leaks closed in order to maintain the desired gas concentration as long as needed.

These fumigants are dangerous to humans, and fumigation jobs must be handled with care during the application and ventilated properly when the treatment is completed. Hydrocyanic acid is deadly to humans and especially dangerous because it is nearly odorless. Chloropicrin, even in minute quantities, is distressing and virtually incapacitating to humans because of its penetrating odor and irritating properties.

Repellents are used to keep insects away from something and are not necessarily toxic. Naphthalene and camphor have been used for decades in homes for keeping insects out of stored clothing. Creosote is used to keep termites out of wood.

Of many compounds that have been tested as repellents of mosquitoes, other biting flies, and chiggers, the most effective are dimethyl phthalate, Indalone, and an organic compound known as Rutgers 612. Each of these compounds is effective against only a certain number of species, but a mixture of the three applied to clothing and skin gives fair protection to the user for a short period. Dimethyl phthalate and other repellents act primarily as a killing agent on mites rather than as true repellents. Benzyl benzoate is proving especially effective for giving protection against mites.

Injury. Insecticides must be used with caution, because they may damage the host as well as the insects or leave a residue that is toxic to man or domestic animals. For instance, lead arsenate sprays that are safe to use on many crops will burn peach and cotton foliage; on these calcium arsenate or a milder compound must be used. Apples sprayed with arsenicals must be washed or cleaned before being eaten,

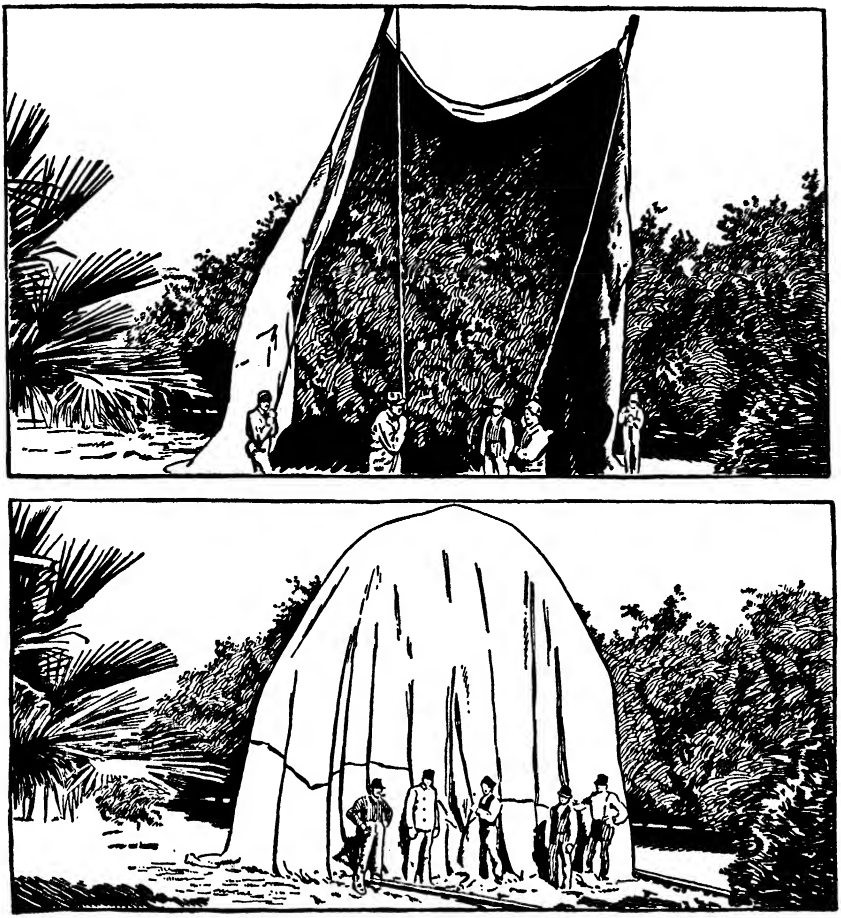

Fig. 434. Tents used for fumigation of citrus trees with hydrocyanic acid gas. Above, preparing the temporary tent; below, the tent in position for fumigation (early illustrations of the method). This method, developed before 1900, is extremely sedentary compared with airplane insecticide application, but is nevertheless one of the most effective methods today for treating insect enemies of citrus trees. (From U.S.D.A., B.E.P.Q.)

because the arsenical residue on the apple is toxic to humans. Oil sprays cause burning of foliage if applied in too concentrated form, and some insecticidal preparations may cause blistering and dermatitis on animals.

Residual Action. An important characteristic of insecticides is the length of time they remain toxic after being applied. Most stomach poison remain toxic for long periods and are spoken of as having a high residual action. Nicotine alkaloid and pyrethrum have practically no residual action, losing their potency almost immediately after they are applied, owing to chemical deterioration. Some of the synthetic contact poisons, such as DDT, have a high residual action. The length of residual action governs to a large extent the frequency with which the insecticide must be reapplied.

Plant Conditioning. We have mentioned that certain sprays such as Bordeaux mixture induce a poisoning of plant sap that is toxic to insects. There are other cases of somewhat similar results that are thought to be due to induced physiological change of the plant, such as plant acidity or alkalinity. An example is the reaction of certain arsenicals on cotton. After being treated with acid calcium arsenate, cotton is unusually susceptible to the cotton aphid, which multiplies in great numbers. On the other hand, cotton treated with basic copper arsenate normally suffers no more than ordinary attack by the cotton aphid. The nature of this plant conditioning is not fully understood, but it promises to be an interesting and profitable field for investigation.

Application. Putting or getting an insecticide where it will do the most good presents problems of many kinds. First, the insecticide must be applied at the correct season and in some cases (as with mosquito larvae) within a period of only a few days. In the second place, weather conditions must be considered, because sprays and dusts cannot be applied during rains or in high winds, and some crops are more susceptible to insecticide burning during periods of high temperature and humidity.

A specialized set of machinery is available for applying sprays, dusts, and aerosols, for dipping cattle, or administering fumigation materials. A careful choice of these must be made for each control project, the area and local condition being taken into consideration, such as topography, height and spacing of the crop, and labor conditions.

CONTROL PROBLEMS

In reviewing the question of insect control there are some pertinent general considerations that must be borne in mind.

Cost. We have already mentioned that biological-control programs are carried on and financed by state or Federal agencies. There are other control projects of such great magnitude and such significance nationally that they are planned and financed by these same agencies. For example, about 1929 the Mediterranean fruit fly became established in Florida and was recognized as a pest that might ruin the American citrus fruit industry. Immediately a Government project was initiated to attempt the eradication of the pest. Quarantines were set up, cleanup measures enforced, thousands of tons of suspected fruit destroyed, and exhaustive surveys made. The fly colony apparently was completely extirpated, and the Nation bore the cost. Periodic grasshopper outbreaks threaten to consume all growing crops in entire states; here the Federal Government assists the farmers by supplying materials and machinery to fight a menace national in scope.

But to the householder with moths in the closet, the farmer with his usual array of insect enemies, the mill operator with bugs in his products, in short, to everyone faced with the necessity of controlling insects by his own efforts, cost is a paramount consideration. The control cost must be low enough to allow the control application to be profitable. If, for instance, an insect threatened to reduce the yield of corn 10 bushels per acre, and a control program would avert 80 per cent of this loss, control cost per acre would have to be less that the price of 8 bushels of corn. Otherwise control would not be attempted, because, if it were, either the farmer would break even on the deal and be out the extra work involved, or he would lose money. The same principle holds with all control done by private means.

In devising control methods, therefore, the entomologist must always strive for practical ones from the cost standpoint. With low-priced crops such as field crops, which seldom have a value of more than $300 per acre, the premium is definitely on low-cost control even at a sacrifice of some efficiency in control obtained. In the case of greenhouse crops, the cash value of the product may be $10,000 or more per acre of glass, and the market price may drop disastrously with only a small insect infestation. Here the demand is for perfect control even at a high price.

The Weakest Link. In order to achieve most in both efficiency and economy, it is necessary to apply control measures at that point in the life history when the insect is most vulnerable or control is most practical. In the life history of many insects there is a point when the insect may be reached easily by control applications. The cabbageworm, for example, is vulnerable at any time during its larval stage to poisons applied to its host. In the codling moth this vulnerable period is much shorter, being the interval of larval life between hatching and entrance of the young larva into an apple. Here the control is applied. An insecticide with a high residual action, such as lead arsenate or DDT, is applied that will cover the late blossoms or fruit. The young larvae will be caught in their attempt to enter an apple, either by eating a little arsenate as they bite through the apple skin, or by contact with the DDT.

During chinch bug outbreaks, it is impractical, because of expense, to apply an insecticide to all the acreage of grass or grain that harbors the bugs. When, however, the bugs migrate from these crops to corn, it is practical to put a repellent barrier or a strip of insecticidal material along a line that the bugs must cross to reach a new food supply. In this way a small strip of applied insecticide is an effective control of millions of bugs on the march.

Community Projects. In the case of some insects it does one person little good to effect control on his premises if the neighbors for some distance around fail to do the same. The ox-warble or cattle grub is easily controlled by squeezing the full-grown larvae out of the pockets they make beneath the hide of the cow and killing them, even though this method of control does little for the immediate season, since the damage is already done. But, if the neighbors don't do it, warble flies from their cattle will fly over and reinfest those of a person who has attempted control. If done thoroughly over a large section of country, the destruction of this year's warbles will prevent their recurrence next year. The same is true of the control of many species of pest mosquitoes; coordinated control over a large area is usually necessary for relief. In this case, however, the control need is annual.

Dispersal of Information: Extension. To be successful, insect control must be based on a detailed knowledge of the insects, local conditions, and possible control methods; and any one of these can change in many details from year to year. Most of the control, moreover, must be done by individuals who are not specially trained in the work and who do not have this information readily available. To put the known information into the hands of these people is the field of *extension.* The information must be timely and simply but plainly stated and must reflect up-to-date advances in combating pests.

It is being recognized more and more that extension is a vital phase of insect control. A good control practice not put to use does no good. Extension methods now embrace practically every known way of getting pertinent information to those who need or want it. State and Federal agencies, private research centers, and industrial concerns aid in carrying on the work. Bulletins, circulars, and newsletters are employed more than anything else, supplemented by radio talks, magazine and newspaper releases, lectures, and field demonstrations. By these efforts it is hoped ultimately that in the United States everyone with an insect-control problem will be able to find the best known way to handle it.

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